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Trends in Fishing Mortality Rate along with Errors in Natural Mortality Rate can cause Spurious Time Trends in Fish Stock Abundances Estimated by Virtual Population Analysis (VPA)

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Lapointe, M. F., R. M. Peterman, and A. D. MacCall. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Can. J. Fish. Aquat. Sci. 46: 2129–2139.

Many researchers have reported biases in estimates of fish abundance reconstructed by virtual population analysis (VPA). We document that VPA can produce changing levels of bias through time, thereby creating spurious time trends in recruitment and stock biomass estimates. We generated catch data from empirically based simulations of nine fish populations, estimated abundances using VPA with a deliberately mis-specified natural mortality rate, *M*, and compared the estimates to the models' "true" abundances. A period of increasing fishing mortality rate, *F*, combined with an overestimate of *M*, produced spurious decreasing time trends in estimated abundance and recruitment, even when the true time series of *F* was known. Analogously, an underestimate of *M* led to a spurious increasing time trend. Bias was increased by a higher true *M*, and (for a given total change in *F*) by a slower increase in *F*. Because field estimates of *M* are uncertain and trends in *F* are common, some apparent trends (or lack of them) in abundances reconstructed by VPA may be artifacts. Therefore, inferences about the results of past management actions and about physical or biological effects on variability in recruitment must be made cautiously when VPA estimates are used.

De nombreux chercheurs ont signalé l'existence de biais dans les estimations des effectifs de poissons réalisées par l'analyse des populations virtuelles (VPA). Nous soutenons que les biais inhérents à l'exécution de la VPA peuvent varier dans le temps, introduisant ainsi de fausses tendances temporelles dans les estimations du recrutement et de la biomasse des stocks. Nous avons produit des données sur les captures à partir de simulations empiriques de neuf populations de poissons, estimé les effectifs au moyen de la VPA fondée sur un taux de mortalité naturelle délibérément faussé (*M*) et comparé les estimations aux effectifs « véritables » calculés par les modèles. Une période d'accroissement du taux de mortalité due à la pêche (*F*), alliée à une surestimation de *M*, a engendré des tendances temporelles anormalement décroissantes dans les estimations des effectifs et du recrutement, même quand la véritable série chronologique de *F* était connue. En corollaire, la sous-estimation de *M* a produit une fausse tendance temporelle croissante. Le biais augmentait quand le véritable taux de mortalité naturelle augmentait et quand la valeur de *F* croissait plus lentement (pour un changement total donné de cette valeur). Puisque les estimations de M sur le terrain sont peu sûres et que les tendances de la valeur de *F* sont courantes, la présence — ou l'absence — de tendances apparentes dans les effectifs établis par la VPA pourrait bien être artificielle. En conséquence, quand on utilise les estimations produites par la VPA, il importe d'user de prudence pour faire des inférences relatives aux résultats d'activités de gestion passées et aux effets des conditions physiques ou biologiques sur la variabilité des taux de recrutement.

Received November 17, 1988
Accepted August 1, 1989
(J9943)

Reçu le 17 novembre 1988
Accepté le 1 août 1989

Virtual population analysis (VPA) and related sequential population estimation techniques (Gulland 1983; Murphy 1965; Pope 1972; Rivard 1983; MacCall 1986) are widely used to reconstruct abundances of fish stocks. This reconstruction is an important component of standard procedures of many fisheries management agencies for estimating stock sizes, forecasting catches, and evaluating the success of past management schemes (Pope and Shepherd 1985; Rivard and Foy 1987).

The effects of using incorrect parameter values in VPA have been studied extensively (e.g. Pope 1972; Agger et al. 1973; Ulltang 1977; Sims 1984; Hilden 1988). It is well known from these and other papers that errors in the instantaneous natural mortality rate, M, and the instantaneous terminal fishing mortality rate, F_L, can create erroneous abundance estimates of both recruits and stock biomass, and that the effect of errors in F_L is reduced by large cumulative fishing mortality. In addition, errors in reported catches or in estimated weights and ages of fish can also lead to incorrect abundances (Pope and Gray 1983; Rivard 1983; Rivard and Foy 1987). Because of these sources of error, several authors have derived confidence intervals for

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abundances estimated by VPA under various types of uncertainty in inputs to VPA (e.g. Pope 1972; Prager and MacCall 1988; Sampson 1987, 1988; Kimura 1989). Under certain conditions, errors in M, F_L or both can also create spurious time trends in abundance (Rivard 1983; Hilden 1988; Sampson 1988; Bradford and Peterman 1989); i.e. even if true recruits and stock biomass were constant, such errors in the parameters of VPA would lead to a time trend in abundance estimates. Time trends in estimated abundance are especially relevant for, (1) evaluations of past management regulations based on the estimated response of the population, and (2) research on mechanisms causing temporal variation in recruitment.

The purpose of this paper is to document a much wider range of situations than previously reported in which spurious time trends in estimated abundances can occur. Specifically, if there are increasing trends in F in any part of the time series of catch data, and if an error exists in the M used in VPA, abundances reconstructed by VPA will have a spurious time trend.

Increasing time trends in F are common in many commercial fisheries (e.g. Hoag and McNaughton 1978; Anderson and Paciorkowski 1980; Winters et al. 1985; Espino and Wosnitza-Mendo 1986; Ahrenholz et al. 1987). These trends may result from a variety of mechanisms including increases in fleet size, "fishing-up" (the removal of accumulated stock, particularly old age classes) early in the development of a fishery (e.g. Ricker 1973; Francis 1986), use of nominal or incompletely standardized effort data which contain trends in fishing power, depensatory catchability coupled with decreases in stock size (e.g. clupeoids; MacCall 1976; Ulltang 1976), and others. Results from VPA often show increasing time trends in fishing mortality rates. However, as we document below, VPA will not correctly identify or account for such trends if there is an error in one or more of the parameters input to VPA, because trends in F exaggerate the effect of those errors in a different way than documented previously. Hilden (1988) showed that increasing trends in F biased recruitment estimates obtained from VPA, but he did not quantify their effect on time trends in recruitment or total stock biomass estimates. Analysts can, in theory, delete data covering years of increasing F from a catch data set before running VPA, but in practice there may be too few years of data left after deletion to be useful.

Methods

In nature, the true abundance of a fish stock will always be uncertain. Therefore, to investigate the impact of increasing trends in F on VPA, we used a simulation model to generate synthetic (i.e. "true") abundances that were known exactly. We focused our analyses on trends of increasing F with time, because they are the most common.

Historical F trends have differed among stocks, varying from small to large ranges in absolute F and short to long periods over which F changes occurred. Therefore, to generalize our findings, we based our analysis on nine different stocks.

The general procedure was:

1. Generate a time series of simulated "true" abundance and catch data from a population model, using known parameters and a time series of increasing fishing mortality rates to simulate the trends in F (called an "F scenario").
2. Estimate annual abundances using iterative VPA (Rivard 1983) given: (a) the catches generated by the simulation of the population model, (b) the true time series of fishing mortality rates, and (c) an incorrect M^{VPA} (henceforth, parameters with a VPA superscript will refer to the parameter values input to VPA, and those without superscripts will be the true values used in the simulation to generate the catch data).
3. Compare time trends of estimated and true abundances (recruits and biomasses).

The specifics of this procedure are as follows.

Simulated Populations and F Scenarios

Simulated populations were generated using parameters (fishing and natural mortality rates, age-specific selectivities, and weights-at-age) from nine stocks (Table 1). We chose these stocks as examples of fishes with different life histories, age-specific selection coefficients, and F trends. We used the parameter values in Tables 2 and 3 as well as others drawn from the references in Table 1. Populations were simulated using the following approach.

Recruitment (number of fish in the youngest fished age) was assumed constant at 1×10^6 fish (we relax this assumption later in the Sensitivity Analysis section), and numbers of fish in older ages were calculated using

$$(1) \quad N_{i+1} = N_i e^{-Z_i},$$

where N is the initial number of fish of age i and $Z_i = M + F_i$. M and F_i are the instantaneous annual natural mortality rate and age-specific fishing mortality rate, respectively. We assumed that the population had been fished at the minimum F prior to the start of each F scenario (see below).

Age-specific fishing mortality rates were calculated as

$$(2) \quad F_i = s_i F_L,$$

where the s_i's are the age-specific selection coefficients and F_L is the fishing mortality rate for the oldest age in a given year. F_L's for each year were determined from scenarios used to simulate periods of increasing F (see below). By assuming that the time series of F_L was known exactly for VPA, we were able to document the minimum qualitative effects of errors in M^{VPA}. We relax this assumption of known F_L later.

Stock biomass in each year was calculated as

$$(3) \quad B_t = \sum_i N_i w_i,$$

where w_i are the weights at each age in kilograms.

Simulated catches were generated using the Baranov catch equation (Ricker 1975).

$$(4) \quad C_i = \frac{N_i F_i (1 - e^{-Z_i})}{Z_i},$$

where C_i is the number of fish caught at age i.

We used two different F scenarios. In the first scenario, we used increasing F trends estimated from the historical data for each stock, to explore the relative magnitude of potential bias in abundance estimates for historical situations. Each historical F pattern was approximated with a linear trend using the observed maximum and minimum F values (F_{max} and F_{min}) and the actual number of years of increasing F observed for each stock (Table 3). In the second scenario, we applied a common F trend to all stocks to generalize our results by exploring how the bias in estimated abundances was affected by different life history characteristics. In both F scenarios, F_L for each year was calculated using

TABLE 1. Sources of data used to generalize effects of input errors to VPA across stocks.

Common name	Location	Species	Abbreviation	Source
Atlantic mackerel	ICNAF areas 3–6	*Scomber scombrus*	Mac	Anderson and Paciorkowski (1980)
Atlantic menhaden	East coast, US.	*Brevoortia tyrannus*	Men	Hightower and Grossman (1985) Arenholz et al. (1987)
Dover sole	Oregon	*Microstomus pacificus*	Dov	Hayman et al. (1980)
Fortune Bay herring	Fortune Bay, Nfld.	*Clupea harengus*	FBH	Winters et al. (1985)
Pacific cod	Hecate Strait, B.C.	*Gadus macrocephalus*	Cod	Fournier (1983)
Pacific halibut	Area 3	*Hippoglossus stenolepis*	Hal	Hoag and McNaughton (1978)
Pacific ocean perch	Queen Charlotte Sound, B.C.	*Sebastes alutus*	POP	Hightower and Grossman (1985) Archibald et al. (1983)
West Scotland herring	ICES area VIa	*Clupea harengus*	WSH	Saville and Bailey (1980)
Yellowfin sole	Eastern Bering Sea	*Limanda aspera*	Yel	Wakabayashi (1984)

TABLE 2. Parameter values for nine different marine fish stocks used in the analysis. Abbreviations of stock names in the top row are defined in Table 1, where literature sources are also given. M is the instantaneous annual natural mortality rate. Selection coefficients (i.e. s_i) of partial recruitment to the fishery are given for each fished age, scaled so that the coefficient for the last fished age class is 1.0 in all cases. Unfished ages are shown by a hyphen.

	Stock								
	Mac	Men	Dov	FBH	Cod	Hal	POP	WSH	Yel
M	0.3	0.45	0.2	0.2	0.65	0.2	0.05	0.1	0.25
Age	Selection coefficients								
0	—	0.34	—	—	—	—	—	0.22	—
1	0.12	1.06	—	—	—	—	—	0.33	—
2	0.37	0.93	—	0.14	0.14	—	—	0.60	—
3	0.63	0.91	—	0.52	0.48	—	—	0.82	—
4	0.78	0.84	—	0.86	0.76	—	—	0.81	—
5	0.80	1.07	—	1.09	0.92	—	—	0.81	0.04
6	0.77	1.00	0.48	1.08	1.00	—	0.05	0.85	0.17
7	0.92	1.00	0.61	1.07	1.00	—	0.11	0.95	0.33
8	0.97	—	0.67	1.05	1.00	0.14	0.21	0.98	0.56
9	1.00	—	0.80	1.03	1.00	0.29	0.36	1.00	0.73
10	—	—	0.89	1.02	—	0.41	0.58	—	0.88
11	—	—	0.95	1.00	—	0.55	0.85	—	0.97
12	—	—	1.08	—	—	0.68	1.14	—	1.00
13	—	—	1.00	—	—	0.90	1.40	—	1.00
14	—	—	—	—	—	0.92	1.56	—	1.00
15	—	—	—	—	—	1.00	1.60	—	1.00
16	—	—	—	—	—	1.00	1.50	—	1.00
17	—	—	—	—	—	1.00	1.28	—	1.00
18	—	—	—	—	—	1.00	1.00	—	—
19	—	—	—	—	—	1.00	1.00	—	—
20	—	—	—	—	—	1.00	1.00	—	—
21	—	—	—	—	—	—	1.00	—	—
22	—	—	—	—	—	—	1.00	—	—
23	—	—	—	—	—	—	1.00	—	—
24	—	—	—	—	—	—	1.00	—	—
25	—	—	—	—	—	—	1.00	—	—
26	—	—	—	—	—	—	1.00	—	—
27	—	—	—	—	—	—	1.00	—	—
28	—	—	—	—	—	—	1.00	—	—
29	—	—	—	—	—	—	1.00	—	—

$$(5)\quad F_{L,t} = F_{L,t-1} + \left(\frac{F_{max} - F_{min}}{T_f}\right) \text{ for } t<T_f,$$

where $F_{L,t}$ is the fishing mortality in year t for the oldest age, T_f is the duration (years) of increasing F for each scenario, and $F_{L,0} = F_{\min}$ for all scenarios. For the historical scenarios, $F_{\min}$, $F_{\max}$, and T_f were different for each stock (Table 3). For the common F scenarios, all stocks had $F_{\min} = 0.1$, $F_{\max} = 1.0$, and T_f = one of the values between 5 and 30 yr, in 5-yr intervals. The purpose of varying T_f in different model runs of the common F scenarios was to explore the effects of a wide range of rates of change in fishing intensities (rapid to slow increases in F). For each T_f, we calculated the rate of change in F per year (i.e. $\Delta F\cdot\text{yr}^{-1} = [(F_{\max} - F_{\min})/T_f]$). In both the common and historical scenarios, we set $F_L = F_{\max}$ after the period of increasing F and for the remainder of the simulation (i.e. for all $t \geq T_f$).

Estimated Populations

Populations were estimated using VPA in the standard formulation shown below (Gulland 1983, p. 105). First, the number of fish in the oldest (L) age class in each year was estimated from

$$(6)\quad N_i = \frac{C_i Z_L^{VPA}}{F_L\,(1 - e^{-Z_L^{VPA}})},$$

where $Z_L^{\text{VPA}} = F_L + M^{\text{VPA}}$, and F_L for each year was determined from equation (5) above. Thus, we assumed that the true time series of F_L values was known. F_i values for each of the younger ages in each cohort were calculated by finding the solution to

$$(7)\quad \frac{N_{i+1}}{C_i} = \frac{Z_i^{\text{VPA}}\,e^{-Z_i^{\text{VPA}}}}{F_i\,(1 - e^{-Z_i^{\text{VPA}}})},$$

which comes from solving equation (1) for N_i, and substituting the result for the left hand side of equation (6). Equation (7) was solved for F_i using Muller's (1956) method available in the IMSL subroutine ZREAL1 (IMSL 1982). Starting values for the subroutine were estimated from

$$(8)\quad F_i = \log_e(N_i/N_{i+1}) - M^{\text{VPA}},$$

where the N_i was calculated using Pope's (1972) cohort analysis approximation,

$$(9)\quad N_i = N_{i+1}e^{M^{\text{VPA}}} + C_i e^{(M^{\text{VPA}}/2)}.$$

F_i values from solving equation (7) were then used in equation (10) along with M^{VPA} to solve for N_i

$$(10)\quad N_i = N_{i+1}/e^{-Z_i^{\text{VPA}}}.$$

This process was repeated for each cohort, working backwards in time in the usual fashion. We used the iterative method of Rivard (1983) in which new age-specific selection coefficients were calculated from the table of F_i estimates and the VPA was repeated until selection coefficients from successive iterations converged. The age-specific selection coefficients were used in

TABLE 3. For each of the nine stocks studied here, we show from left to right the assumed true instantaneous natural mortality rate, M, and six characteristics of the historical F scenarios: the observed minimum and maximum F ($F_{\min}$ and $F_{\max}$), duration of the period of increasing F, range in cumulative F values between cohorts at the start and end of the period of increasing F, and the rate of change in F per year (unscaled and then scaled relative to M).

Stock	True M	$F_{\min}$	$F_{\max}$	Years of increasing F (T_f)	Range in cumulative F	$\Delta F \cdot yr^{-1}$	$\Delta F \cdot yr^{-1} \cdot M^{-1}$
Atlantic mackerel	0.30	0.05	0.85	10	2.074	0.08	0.27
Atlantic menhaden	0.45	0.70	3.00	6	4.359	0.38	0.85
Dover sole	0.20	0.12	0.25	9	0.371	0.01	0.07
Fortune Bay herring	0.20	0.02	1.00	6	1.408	0.16	0.82
Pacific cod	0.65	0.22	0.76	6	0.700	0.09	0.14
Pacific halibut	0.20	0.11	0.30	12	0.591	0.02	0.08
Pacific ocean perch	0.05	0.05	0.35	3	0.022	0.10	2.00
West Scotland herring	0.10	0.20	1.10	8	1.654	0.11	1.12
Yellowfin sole	0.25	0.08	0.29	4	0.040	0.05	0.21

equation (2) to calculate the terminal F values for incomplete cohorts (cohorts that had not yet reached the oldest fished age by the last, or most recent, year of the catch data). F_i values for younger ages of complete cohorts were obtained from equation (7) and remained unchanged after iterations. Thus, the iterative method we used only affected abundance estimates for the incomplete cohorts.

In each case, the time series of F_L's given to the VPA was identical to that used in the simulated population, and the catches were those generated by the simulation. The only error introduced into VPA was through the value of M^{VPA}; we used $M \pm 50\%$. We chose to solve the VPA equations exactly using the IMSL routine because with this range in errors, the incorrect M^{VPA} values for some stocks were outside of the range of acceptable values for either Pope's (1972) or MacCall's (1986) approximations.

Comparison of Estimated and True Abundances

We compared the true abundances with those estimated by VPA using the following index of percent spurious change, P_S,

$$(11) \quad P_S = P_E - P_T,$$

which was the difference between the percentage change in estimated abundances (P_E) over the course of the simulation and the percentage change in true abundances (P_T) over the same period. We used percent change as our index because it was a general measure of the bias that was also proportional to the absolute change per year in recruits or biomass. P_E and P_T were calculated as

$$(12) \quad P_E = \frac{NE_t - NE_1}{NE_1} \cdot 100$$

and

$$(13) \quad P_T = \frac{NT_t - NT_1}{NT_1} \cdot 100,$$

where NT_1 and NE_1 were the true and estimated initial abundances at time $t=1$, respectively, and NT_t and NE_t were the stabilized abundances following the period of increasing F. The latter abundances occurred at time $t=T_f$ for recruitment, and $t=T_f+k-1$ for biomass, where k is the number of ages fished for each stock. We generated catch data for T_f+2k-2 yr to ensure that stabilized abundances were estimated from cohorts that had reached the oldest fished age. Thus, we only used the abundance estimates obtained from "complete" cohorts in our calculations.

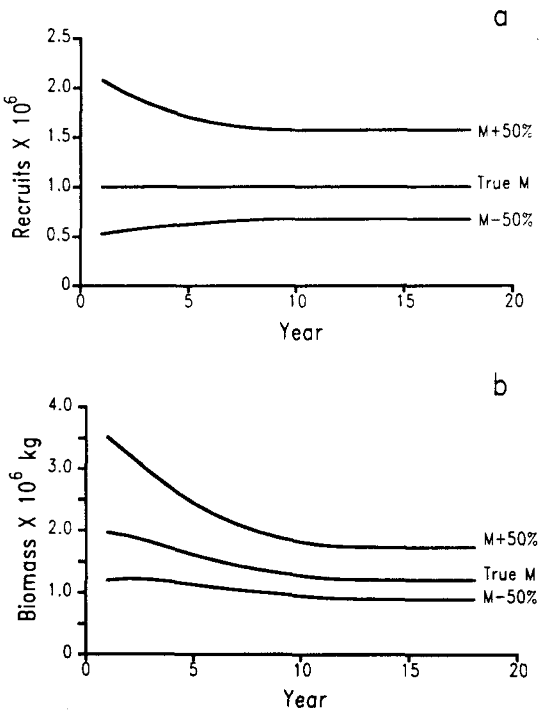

FIG. 1. Time series of Atlantic mackerel recruits and total stock biomass using the historical F trend for that stock. Part (a) shows true recruits (middle line) and recruits estimated by VPA when the natural mortality rate used in VPA (M^{VPA}) was 50% above the true value, M, (top line) or 50% below M (bottom line). Part (b) shows true stock biomass (middle line) and biomass estimated when M^{VPA} was 50% above M (top line) or 50% below M (bottom line). VPA estimation proceeded from the right side of the figure to the left.

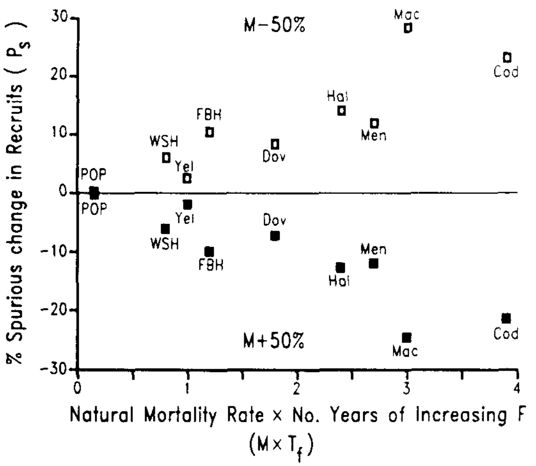

FIG. 2. Percent spurious change (increase or decrease) in abundance of recruits estimated by VPA when M^{VPA} was 50% below M (top half; $r^2=0.78$, $P<0.002$) or 50% above M (bottom half; $r^2=0.81$, $P<0.002$). Stock abbreviations are defined in Table 1. For each stock, the true M value, duration of the period increasing F (T_f), F_{min} and F_{max} are for the historical scenarios (Table 3).

We refer to P_T and P_E as the true and estimated change in abundance and P_S as the spurious change or spurious trend. We calculated each of these three quantities for both recruits and stock biomass. In the case of recruitment, $P_S=P_E$ because P_T, the true trend, was 0 (i.e. we assumed constant recruitment in our simulations). Thus, in our results below, $P_S>0$ for recruitment meant that VPA estimated a false increasing time trend in recruits, whereas $P_S<0$ would come from a spurious decreasing trend. However, for stock biomass, increases in F cause a decline in both the simulated (i.e. true) and estimated biomass as older age classes are depleted from the initial stock. Thus, $P_S>0$ for stock biomass meant that VPA underestimated the true percentage decline in biomass. For example, $P_E=-20\%$ for biomass and $P_T=-30\%$ gives $P_S=+10\%$ from equation (11). In contrast, $P_S<0$ indicated an overestimate of the decline in biomass.

Results

Historical *F* Scenarios

Figure 1 shows results for Atlantic mackerel (*Scomber scombrus*) at various M^{VPA} values when the historically observed F scenario was applied. When M^{VPA} equalled the true M, VPA correctly estimated the true recruitment and true stock biomass (middle lines in Figs. 1a and 1b). Therefore, trends in F do not cause VPA to estimate abundance incorrectly when M is known exactly and there are no other errors in VPA inputs. However, when M^{VPA} was incorrect, estimates of recruits and stock biomass diverged from the true values as VPA proceeded back in time through the cohorts (from right to left in Fig. 1). When M^{VPA} was less than M, recruitment and biomass were both underestimated, VPA generated a false increasing time trend in recruits, and underestimated the decreasing trend in biomass (Fig. 1). When M^{VPA} was greater than M, VPA generated spurious decreasing time trends in recruitment, overestimated the percent decline in biomass, and overestimated recruitment and stock biomass (Fig. 1). We found similar results for other stocks; for a given sign of error in M^{VPA}, the spurious change in recruits and biomass for the historical scenarios increased with the product of M and the number of years of increasing F, T_f (Figs. 2 and 3). When M^{VPA} was incorrect, the percent spurious change was greater for recruits than for total stock biomass for a given stock (Figs. 2 and 3).

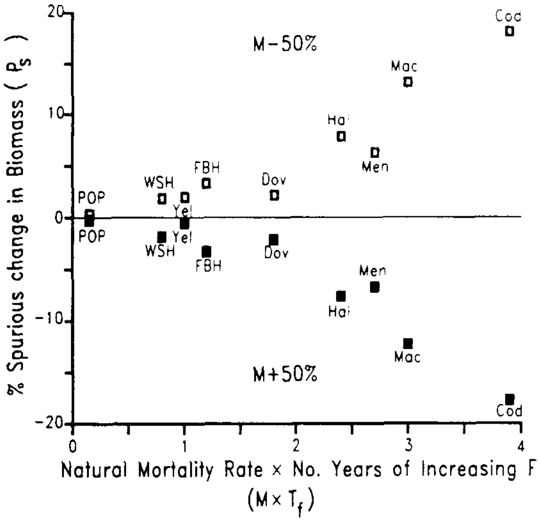

FIG. 3. Same as Fig. 2 except for stock biomass. For $M^{VPA}=M-50\%$, $r^2=0.86$, $P<0.001$ and for $M^{VPA}=M+50\%$, $r^2=0.88$, $P<0.001$.

Explanation of Historical *F* Scenarios

The underlying cause of the time-trend bias is a simple extension of the well-known effects of errors in VPA parameters (Pope 1972; Agger et al. 1973; Ulltang 1977; Sims 1984; Bradford and Peterman 1989; Sampson 1988; Hilden 1988). Pope (1972) showed that for a given M^{VPA}, errors in estimated abundance at a given age caused by an incorrect choice of F_L^{VPA} decreased as the cumulative fishing mortality on the cohort increased. Pope's analysis was extended to include errors in M by Sims (1984), who gave an approximate formula that related the relative error in abundance estimates to the magnitude of error in M^{VPA} and cumulative fishing mortality (see Sims' equation 8). These results imply that identical successive annual cohorts that experience different cumulative fishing mortality rates will have different amounts of bias in recruitment estimates for each successive cohort when these estimates are derived from VPA with an incorrect F_L^{VPA} or M^{VPA}.

Indeed, this is the underlying cause of the spurious time trends in abundance estimates shown in this paper; differences in cumulative fishing mortality rate exist among successive cohorts because of changes in F over time and these are coupled with an incorrect input parameter to VPA, M^{VPA}. This mechanism is detailed below.

A full explanation of the time-trend bias in Fig. 1 requires several steps. (1) For the case of $M^{VPA}=M+50\%$ in Fig. 1a, recruitment estimates in years 10 to 18 were constant but biased above true recruitment; this overestimate was due solely to the error in M^{VPA} because there was no change in F during this period. (2) However, the sequence of fishing mortality rates

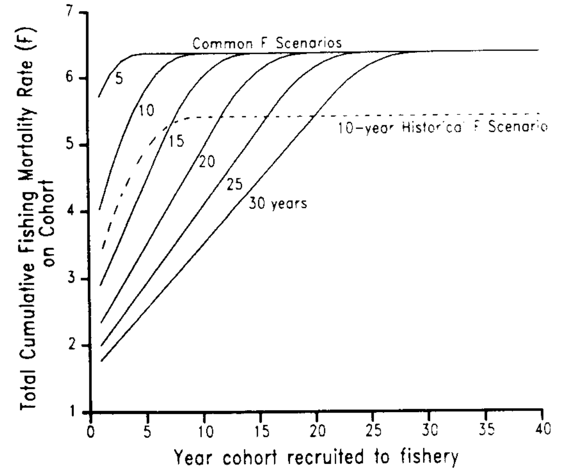

FIG. 4. Total fishing mortality rate (ΣF_i) experienced by each cohort of Atlantic mackerel in simulations using true M and F_i values. Lines are shown for each of the simulated common F scenarios (solid lines) ranging in duration from 5 to 30 yr, and for the 10-yr historical F scenario (dashed line). VPA estimation proceeded from the right side of the figure to the left.

during the period of increasing F caused cohorts that recruited to the fishery in years 1–9 to experience lower cumulative fishing mortality rates (ΣF_i for all fished ages) than cohorts that recruited later (dashed line in Fig. 4). As Sims (1984) noted, the amount of error in an abundance estimate resulting from an error in M^{VPA} is larger when the cumulative fishing mortality experienced by a cohort is small. Thus, the lower cumulative fishing mortality rates on cohorts that recruited in years 1–9 led to more biased abundance estimates in those years. (3) Finally, recruits from each successive cohort that recruited in years 1–9 were estimated with decreasing bias, because as F increased, cumulative fishing mortality rates on each successive cohort increased (Fig. 4 dashed line). In other words, the error in abundance estimates already present due to an incorrect M^{VPA} was exaggerated most in early years when cumulative F was low and least when cumulative F was high, at the end of the period of increasing F. Hence, the result was a time trend in estimated recruitment (Fig. 1a), despite a constant true recruitment and the use of the true time series of F_L by VPA. For brevity, we refer below to this mechanism that explains time trends as "differences in cumulative fishing mortality rate among successive cohorts." In the case of $M^{VPA} = M - 50\%$, the explanations are similar but errors appear as underestimates of true abundance rather than overestimates (bottom of Fig. 1a).

Time trends occur in stock biomass estimates (Fig. 1b) through the same mechanisms as in recruits. However, spurious time trends were generally greater for recruits than for stock biomass because estimates of abundance for younger ages will be more biased in percentage terms than estimates for older ages within the same cohort: as VPA works back through a cohort, these estimates of young ages result from more applications of the incorrect Z^{VPA} in equation (10). Total stock biomass estimates are less biased than recruits because biomasses are the weighted sum of abundances over ages, and the less biased estimates for older ages dilute the effect of the more biased abundance estimates of younger ages.

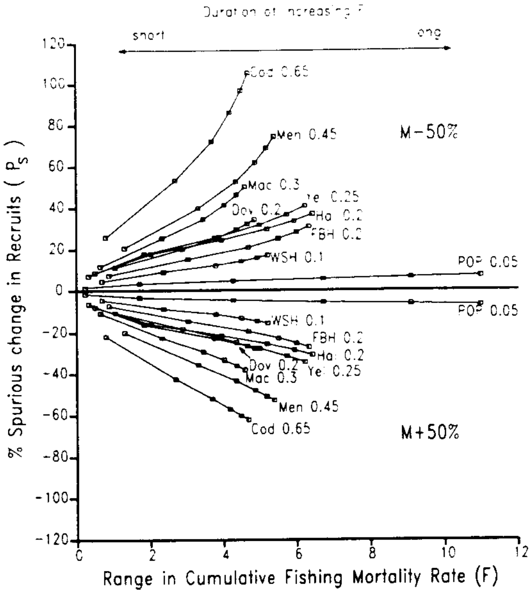

FIG. 5. Percent spurious change (increase or decrease) in abundance of recruits estimated by VPA when M^{VPA} was 50% below M (top half) or 50% above M (bottom half). Curves are for the stocks abbreviated on the right (defined in Table 1) and true M values are beside stock abbreviations. For each stock, the duration of the common F scenarios ranged from 5 yr (left point) to 30 yr (right point) in 5-yr intervals. "Range in cumulative fishing mortality rate" is the maximum cumulative F on cohorts minus the lowest cumulative F encountered in that F scenario (see text).

Spurious change in recruits and biomass increased with the product of M and T_f (Figs. 2 and 3) because for any given stock, longer periods of increasing F result in greater differences in cumulative fishing mortality among successive cohorts (Fig. 4), and because for any given cumulative F, larger M^{VPA} results in more bias (see section "Explanation of comparisons among stocks" below). Thus, $M \cdot T_f$ is an approximate index of the time-trend bias caused by an incorrect M^{VPA} for these historical situations. The index is not perfect because of differences in historical ranges in F and partial recruitment vectors among stocks (Tables 2 and 3).

Common F Scenarios

Comparisons among stocks

One purpose of the common F scenarios was to compare spurious time trends among stocks with different life history characteristics. This was not possible in the previous scenarios because of historical differences in F trends among stocks; in this section, we applied the same sequence of increasing F to all stocks. In these common F scenarios, F_{min} and F_{max} were the same for all durations of increasing F, ranging from 5 to 30 yr, as described above. Because time trends in abundance estimates caused by increasing trends in F in conjunction with an incorrect M^{VPA} result from differences in cumulative fishing mortality among successive cohorts, we calculated a single index of these differences, which was the cumulative fishing mortality rate on cohorts that recruited to the fishery in the year

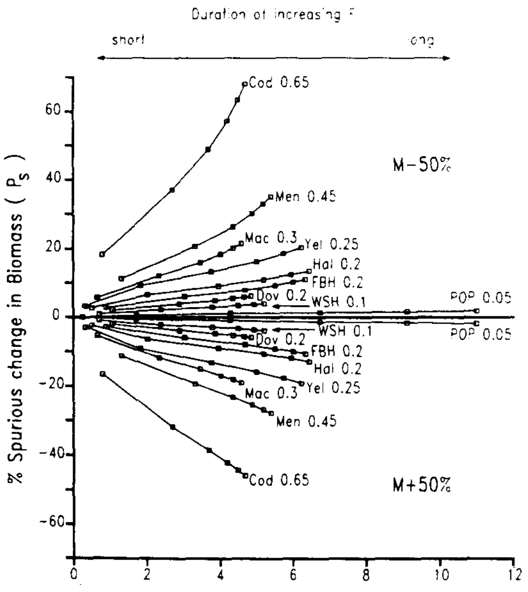

FIG. 6. Same as Fig. 5 except for stock biomass.

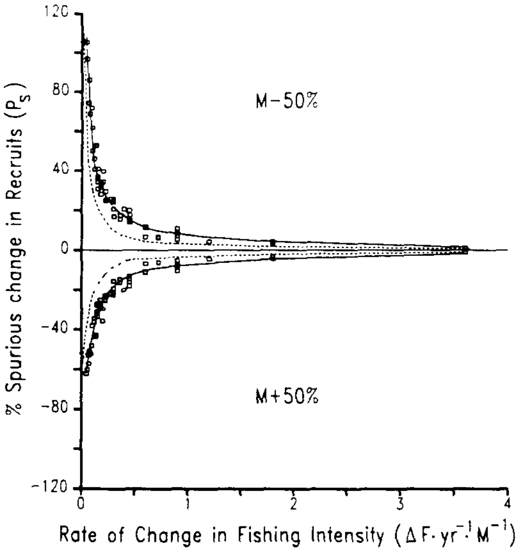

FIG. 7. Percent spurious change in abundance of recruits estimated by VPA in relation to the relative rate of change in fishing intensity (equal to the rate change in F_L per year divided by the true M value for each stock). Top half is for M^{VPA} 50% below M and bottom half is for M^{VPA} 50% above M. Each point in each half represents one stock and one duration of increasing F, with the shortest durations on the right side. Points and outer curves are for F_L ranging from 0.1 to 1.0. Inner dashed curves without points are for F_L ranging from 0.05 to 0.5.

T_f (when $F_L = F_{max}$) minus cumulative F on cohorts that recruited in year 1 (top minus bottom values on a given curve in Fig. 4). This index was specific to the stock and the number of years of increasing F because stocks had varying numbers of exploited age classes and different age-specific selection coefficients and because for any given stock the cumulative fishing mortality on cohorts varies with the numbers of years of increasing F (Fig. 4). We henceforth call this index "the range in cumulative F."

We used the range-in-cumulative-F index to compare the percent spurious change in recruits (Fig. 5) and stock biomass (Fig. 6) across stocks. For each stock, six square points are shown. Each point on a given curve is for a given duration of increasing F, ranging from 5 yr (left-most point on each curve) to 30 yr (right-most point). Long periods of increasing F resulted in the largest absolute values of percent spurious change in abundance estimates within a given stock. Stocks with larger M (e.g. Pacific cod (*Gadus macrocephalus*), menhaden (*Brevoortia tyrannus*)) had greater spurious trends for a given length of increasing-F period than stocks with low M. Trends for high M stocks were also more sensitive to changes in the length of the increasing-F period; high M stocks had a much larger increase in the absolute value of percent spurious change than low M stocks when the rate of change in F was varied from rapid (left ends of curves) to slow (right ends). Three stocks (i.e. Pacific halibut (*Hippoglossus stenolepis*), Dover sole (*Microstomus pacificus*) and yellowfin sole (*Limanda aspera*)) with similar M values had overlapping curves of percent spurious change in recruits. As found for the historical scenarios, recruits had larger absolute values of percent spurious change than biomass for a given situation.

Explanation of comparisons among stocks

First, within each stock, longer periods of increasing F caused larger absolute values of the percent spurious change in abundance estimates than short periods, giving slopes to the curves in Figs. 5 and 6. This was because we assumed F_{min} and F_{max} were constant; the longest durations thus create the lowest cumulative F on cohorts present during the increasing-F phase (e.g. Fig. 4 for mackerel) and as noted above, low cumulative F's give the largest errors in estimated abundance. In the Sensitivity Analysis section below, we remove the assumption of a constant F_{max} and results are similar. Stocks with high M have greater spurious time trends ($|P_S|$) than low M stocks for a given range in cumulative F because errors in abundance estimates for these stocks are inflated more by the larger Z^{VPA} (equation (10)) than estimates for low M stocks.

Similarly, stocks with large M have steeper slopes in Figs. 5 and 6 than stocks with low M (i.e. the former are more sensitive to changes in the duration of the increasing-F phase) because in successive applications of equation (10) in the backwards recursion, the change in errors in N_i resulting from the change in range of cumulative fishing mortality is exaggerated more by the larger Z^{VPA} of large M stocks.

Generalization across stocks

The second purpose of the common F scenarios was to permit generalization of results across stocks. To generalize our findings, we used the variable defined above, $\Delta F \cdot yr^{-1} \cdot M^{-1}$, which is a measure of the rate of change in intensity of F, relative to M. When the results from the common F scenarios for all stocks were combined, we found an inverse relationship between percent spurious change in recruits and this relative rate of change in intensity of exploitation (outer curves and symbols in Fig. 7). However, the same plot for percent spurious change in biomass (Fig. 8) gave a family of curves; stocks with the lowest M values tended to have smaller percent spurious changes. In

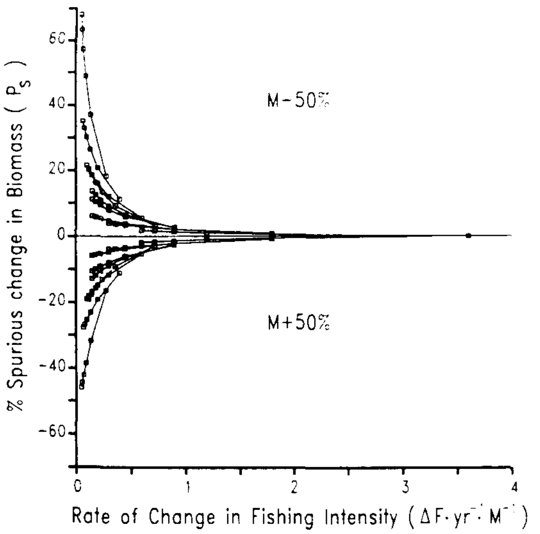

FIG. 8. Same as Fig. 7 except for stock biomass and larger F_i range only. Points of different durations of increasing F are connected for a given stock. Curves for high M stocks have steepest slopes; low M stocks tend to have shallow sloped curves.

both Figs. 7 and 8, the smallest spurious trends came from cases with rapid increases in F.

Explanation of generalization across stocks

The general patterns in Figs. 7 and 8 result from a combination of processes described in previous sections. We noted above why longer periods of increasing F caused larger absolute values of percent spurious change in abundance estimates. Because long periods of increasing F lead to a slow rate of change in F ($\Delta F \cdot yr^{-1}$) in our common F scenarios, the spurious trends in recruits resulting from an incorrect M^{VPA} are largest at the slowest relative rate of change in fishing intensity (Fig. 7).

Biomass trends for the nine stocks showed a similar qualitative pattern (Fig. 8). Again recall that periods of increasing F cause decreasing trends in true biomass as the older age classes are depleted, and therefore the percent spurious change in biomass is the difference between the true and estimated trends (equation (11)). True percentage decreases in biomass, (P_T), were larger for stocks with low M because, (1) all stocks shared the same F scenarios, (2) F constituted a larger portion of Z for these low M cases than for high M stocks, and (3) stocks with low M therefore experienced relatively greater percentage changes in Z as F increased compared with stocks with high M. However, these large true trends were exaggerated less by VPA in stocks with low M than in stocks with high M because low M stocks have a small Z^{VPA} in equation (10). The net result is that the absolute value of the percent spurious change ($|P_S| = |P_E - P_T|$) is smaller for stocks with lower M. While this is the same qualitative pattern as found for trends in recruitment, biomass trends are also affected by other factors, such as differences in the number of fished ages and the weight-at-age vector, which are not captured by our simple measure of relative rate of change in fishing intensity. This is particularly true at low rates of change in F and it leads to the family of curves in Fig. 8.

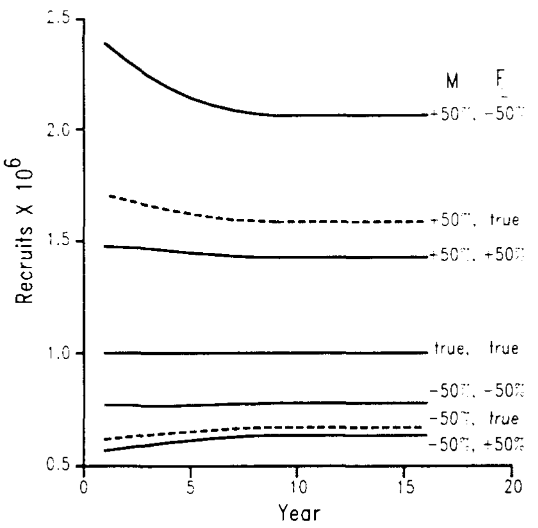

FIG. 9. True recruits (horizontal line) and recruits estimated by VPA under various combinations of errors in M^{VPA} and F_L^{VPA}, for the historical F scenario applied to Dover sole. Dashed curves are for no error in F_L^{VPA} in conjunction with M^{VPA} overestimated (top) or underestimated (bottom) by 50%. Curves for errors in M^{VPA} in conjunction with errors in F_L^{VPA} of ±50% of the true F_L bracket each related dashed curve.

Sensitivity Analyses

Changes in assumed F scenarios

We explored the robustness of our results to changes in some of our assumptions. First, we examined how the absolute range in F_L during the increasing F phase influenced our common F scenario results. Previously, we set $F_{min} = 0.1$ and $F_{max} = 1.0$; here we halved that range (0.05 and 0.5) to generate less intensive exploitation. For a given stock, percent spurious changes in recruits were generally smaller for the lower F_L range, and generalized results across stocks and across durations of increasing F were similar to those for the larger F_L range (inner dashed curves in Fig. 7). The smaller range in F_L created smaller differences in cumulative F among successive cohorts, creating smaller spurious time trends than with the large range. These results are distinct from the effect of F_L values on absolute N_i estimates, which become less biased with large cumulative F (Pope 1972).

Second, in the common F scenarios above we assumed a fixed F_{min} and F_{max} and varied the rate of increase in F by changing the number of years of increasing F. In a sensitivity analysis, we simulated an alternative form of F trend where F_{min} was fixed and F_L increased by a fixed amount each year, resulting in a different F_{max} for each duration of the increasing-F period. The results from these runs had the same qualitative pattern as in Figs. 5 and 6; a longer period of increasing F resulted in greater percent spurious change for the same reason as it did in the main results: it generated a wider range in cumulative F values among cohorts than shorter durations.

Changes in assumed errors

In our simplified analyses in previous sections, we assumed that the time series of F_L was known for doing VPA, but if errors were made in that input, the resulting spurious time trends would be different from those we have shown. We therefore added errors in F_L^{VPA} of ±50% of the true F_L. Simultaneous errors in M^{VPA} and F_L^{VPA} either tended to reduce or exaggerate the effects of the error in M^{VPA} alone, depending on the signs of the two errors (e.g. Dover sole in Fig. 9). This was true of both the absolute error in N_i estimates and the percent spurious change for recruits and stock biomass. Trends due to errors in F_L^{VPA} arise through the same mechanisms (differences in cumulative mortality rate among cohorts) noted previously for errors in M^{VPA}. Because errors in M^{VPA} and F_L^{VPA} are unlikely to cancel one another exactly, some spurious time trend will usually result in practice; its magnitude will depend on the relative magnitudes and signs of errors in M^{VPA} and F_L^{VPA}.

We also considered a fixed absolute error in M^{VPA} (e.g. $M \pm 0.1$) rather than a fixed percentage error and again found the same qualitative pattern as in Figs. 5 and 6 of increasing magnitude of spurious change with longer duration of the period of increasing F.

Decreasing recruitments

To simplify our analysis and explanations, we assumed previously that the decreases in stock biomass that occurred as a result of increasing F did not affect recruitment. This was consistent with the marine fish literature, much of which shows that it is very difficult to detect any response of recruitment to changes in spawning stock biomass over the ranges of observed biomasses (reviewed by Rothschild 1986). For our sensitivity analysis, we examined common F scenario situations in which recruitment decreased each year by a given percentage, paralleling the decrease in stock biomass. When compared with the constant recruitment cases presented above, percent spurious time trends that occurred with decreasing recruitment were smaller by at most one-third (for both recruits and biomass) because decreasing trends occurred in both true and estimated abundances. These results were independent of the direction of error in M^{VPA}.

These sensitivity runs clearly show that spurious time trends in abundances reconstructed by VPA are likely to occur under a wide range of conditions when increasing trends in F are present along with an error in one of the parameters input to VPA.

Discussion

Our results show that in the presence of an error in M^{VPA} and an increasing trend in F_L, VPA generates a spurious time trend in both estimated recruits and stock biomass, even if the actual trend in F_L is known. The magnitude of these false trends is greatest when, for a given M and range in F_L, F increases over a long period, that is, when the percentage change in F_L per year is small (Figs. 7 and 8). This counterintuitive result arises because a slow rate of change in F causes relatively low cumulative F on early cohorts and a wider range in cumulative fishing mortality rates than do rapid F increases, and low cumulative F in turn results in more biased abundance estimates for those early cohorts.

We performed our simulations with a time series of F_L values that approximated the trends in F_L observed historically. However, these observed trends in F are affected by the very bias that we document in this paper; most published tables of F estimates for our stocks came from VPA. Thus, the true rate and magnitude of increasing F trends in our historical scenarios may have been over- or underestimated, and the magnitude of the percent spurious changes may be incorrect for those specific scenarios. Nevertheless, the remainder of our conclusions from using the "common F scenarios" are valid; with any time trend in F_L and an error in M^{VPA}, spurious time trends will be embedded in the resulting abundance estimates.

In our simulations, we assumed that increasing trends in F started at the beginning of the time series of the catch data. If we had generated catch data for years prior to the start of an increase in F, and assumed that F was constant at a minimum level during those years, VPA estimates of recruits and biomass would have continued to diverge from the true values (e.g. Fig. 1) as VPA proceeded back through the cohorts until the cumulative fishing mortalities of successive cohorts were identical (i.e. until the cumulative F on recruits reached a constant minimum level off to the left side of Fig. 4.). The estimated abundance for those early years would therefore be constant. Thus, under such conditions, the spurious trends caused by increasing F would be larger than we have reported here. However, for different durations of the increasing-F period, the estimated abundance in the early years would approach the same plateau of constant bias and therefore the same percent spurious change would result. Such a situation could arise in practice if reliable age-specific catch data were available prior to the start of a time trend in F. However, this may be unlikely because the stimulus for starting to gather data often occurs well into the fishing-up phase in development of a fishery. Even if such data were available, spurious time trends would still exist and the effect of M would be as shown previously. The only change from our results above would occur when comparing two identical stocks that had different durations of increasing F, and where data were available for the period prior to the start of the time trend in F. However, our conclusions concerning the effect of different durations of increasing F will hold whenever longer periods of increasing F result in a greater range in cumulative F (e.g. Figs. 5 and 6).

The spurious time trends that we have documented occur in a wider variety of situations than has been shown previously. First, Hilden (1988) documented false time trends in recruitment in the presence of increasing F trends and an error in M, but he made the additional assumption of an underlying stock–recruitment relationship. In our main analysis, we assumed that no change in recruitment occurred over the range of stock biomasses observed during the simulated periods of increasing F, yet we also found spurious trends due to differences in cumulative F among successive cohorts.

Second, the spurious time trends documented by Bradford and Peterman (1989) arose from using catch data in recent years that included incomplete cohorts (year-classes that had not reached the terminal age by the last year of the catch data), and from using "noniterative" VPA, that is, when the partial recruitment vector of age-specific selectivity coefficients was estimated empirically and the VPA was run only once. Analysts use VPA in this way when major changes in catchability have occurred during the period (e.g. Winters et al. 1985). However, we did not include incomplete cohorts in the simulated catch data here and we used the more common "iterative" VPA (Rivard 1983) instead of noniterative VPA. Our spurious trends resulted from a different and more common mechanism (iterative VPA with increasing F trends and an incorrect M^{VPA}) than the trends in Bradford and Peterman (1989) (noniterative VPA with incomplete cohorts and an incorrect M^{VPA} or F_L^{VPA}). Our results are therefore more general than those of Bradford and Peterman (1989) and Hilden (1988) because false trends will occur even if all incomplete cohorts are removed from the input catch data, even if iterative VPA is used, and without any assumed effect of stock biomass on recruitment.

If noniterative VPA is used with catch data sets that include both incomplete cohorts and periods of increasing F, noniterative VPA will either tend to exaggerate the spurious time trend already documented above due to increasing F trends alone, or will result in spurious trends in the opposite direction, again depending on the signs of errors in M^{VPA} and $F_L{}^{VPA}$ (Bradford and Peterman 1989). Thus, the potential exists for the introduction of complex, nonmonotonic spurious time trends into reconstructed abundances.

We have only addressed increasing F trends but our qualitative results apply more generally to any case in which F tends to increase or decrease (with some variability) over a given period. In the case of a decrease in F, estimates of abundance will converge toward the true value as VPA proceeds back in time through the cohorts, and spurious trends will be opposite in sign from those reported here.

General Implications

These results have considerable relevance for two reasons. First, in practice, M^{VPA} is unlikely to equal the true M. Methods for estimating M for fish populations usually report large confidence intervals (Alverson and Carney 1975; Pauly 1980; Roff 1984; Gunderson and Dygert 1988) or large ranges in different estimates of M for the same species (Vetter 1988), partly because of confounding with other parameters such as the catchability coefficient (Paloheimo 1980). Second, VPA has commonly been used on catch data sets that include periods of increasing F (e.g. references in Table 1 except Fournier (1983) and Archibald et al. (1983)). Thus, the presence of periods of increasing or decreasing trends in fishing mortality rate in past data sets used in VPA may have introduced biases that influenced interpretations of the success or failure of past management actions. As well, studies of mechanisms of variability in recruitment estimated by VPA (e.g. Shepherd et al. 1984; Koslow et al. 1987; Hollowed et al. 1987) and stock–recruitment relations may also have been biased, possibly to the point of masking relationships that were present in nature (Hilden 1988) or creating spurious correlations. Analysts should therefore generate different time series of recruits and stock biomass for each set of parameter estimates used in a VPA. A separate correlation should be performed between the independent variate (such as an environmental factor) and each set of abundance data. Given the natural variability in recruitment and M in nature, and the possibility of time trends in M, it is unlikely that such exercises will identify the true underlying correlations; however, comparisons of results of these different reconstructed time series will demonstrate the sensitivity of such correlations to assumed VPA parameter estimates.

The spurious time trends in abundance estimates caused by increasing F trends may cause problems for some VPA tuning methods, particularly those which use regressions of survey CPUE (catch per unit effort) on VPA estimates (e.g. Rivard 1983; rho method of Pope and Shepherd 1985). Depending on the extent of the F trend bias, the slope from such regressions (i.e. the catchability coefficient) will be biased due to spurious time trends in the estimates from VPA. Therefore, we concur with Mohn (1983) and Pope and Shepherd (1985), who suggest that tuning methods that use effort data are preferable to those that use CPUE data.

Similarly, if spurious time trends in recruitment estimates are present, total allowable catch (TAC) projections will be biased if they are based partly on, (1) projected recruitment from regressions of recruit survey CPUE on VPA recruit estimates (Brander 1987), (2) regressions of VPA recruitment estimates on time (Rivard 1983), or (3) long-term average recruitment (Rivard and Foy 1987). For $M^{VPA}<M$, projected recruitment and biomass will generally be underestimated, there will be a spurious increasing trend in recruitment, and the estimated decrease in biomass will be less than the true decrease. In contrast, for $M^{VPA}>M$, projected recruitment and biomass will be overestimated, recruitment will have a spurious decreasing trend, and the estimated decrease in stock biomass will be greater than the true decrease.

The well known problems with VPA have stimulated the development of nonsequential, statistical fitting methods of estimating abundance, which are now gaining wider acceptance as plausible alternatives to VPA (e.g. Doubleday 1976; Fournier and Archibald 1982; Collie and Sissenwine 1983; Deriso et al. 1985; Gudmundsson 1986; Methot 1989). These methods may be more robust to errors in input parameters, particularly F_L, because they commonly use auxilliary data to help determine estimates. However, most fitting methods require as input an assumed and constant M value and for those which permit estimation of M, M estimates are poorly determined (e.g. Fournier 1983) and very sensitive to errors in other inputs (e.g. aging errors; Fournier and Archibald 1982). Thus, while it is clear that nonsequential techniques will produce biased abundance estimates when M is incorrect, it is not clear whether errors in input parameters will lead to spurious time trends in estimates obtained from such techniques. Therefore, analysts must determine how sensitive abundances estimated by the new fitting methods are to errors in input information. The history of VPA work clearly demonstrates the necessity of such sensitivity analyses; in recent years, analytical and numerical analysis techniques have shown that under certain commonly found circumstances, VPA outputs are quite sensitive to errors in inputs and assumptions (e.g. Ulltang 1977; Sims 1984; Rivard and Foy 1987; Sampson 1987; 1988; Kimura 1989; Bradford and Peterman 1989). These same techniques should be used in rigorous evaluations of the new statistical fitting methods that some researchers hope will replace VPA. Some evaluations have been done (e.g. Deriso et al. 1989) but they should also include cases in which trends in F occur.

Regardless of which stock reconstruction method analysts use, our results and others noted above emphasize the importance of presenting to fishery managers the results of sensitivity analyses when parameters are uncertain. Such information is essential to enable managers to make the best possible decisions, given the large uncertainty in our understanding of these systems. As well, it is essential that more effort be directed at obtaining more precise and accurate estimates of data used in analyses, especially key parameters such as M, because no stock reconstruction method can completely avoid bias if parameter estimates are poor.

Acknowledgments

Michael Bradford, Jeremy Collie, and three anonymous reviewers as well as Geoff Evans, made useful suggestions on a draft manuscript. Funding was provided by an operating grant to R. M. Peterman from the Natural Sciences and Engineering Research Council of Canada and a Special Research Projects Grant from Simon Fraser University.

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