

Abstract.—For fish populations with an annual breeding cycle, a biological reference point based on the Leslie matrix is presented and compared with percent maximum spawning potential (%MSP) and F_{med} reference points. For deterministic population projections, the reference point is defined as the level of fishing mortality (F_{st}) that results in a Leslie matrix with a dominant eigenvalue (i.e. finite rate of increase or λ) of 1.0. It is shown that for the same input data, F_{st} is similar to a reference point based on a %MSP approach. For populations that are growing or declining, however, populations with the same λ but with different age-specific selectivities have different levels of %MSP. Previous applications of this reference point are extended to include situations where recruitment is a stochastic process. In stochastic projections, F_{st} is defined as the level of fishing mortality that results in an average finite rate of increase of 1.0. In an example with Georges Bank haddock, a deterministic analysis with mean birth and death rates resulted in an estimate of F_{st} of 0.52. The same estimate of F_{st} was obtained in a stochastic projection in which the growth rate of the mean population size was used. Stochastic projections using the mean of the finite rates of increase resulted in a lower estimate of F_{st} (0.45). When the value of recruits per unit of spawning stock biomass used in the %MSP analysis was calculated as $\Sigma \text{recruits} / \Sigma \text{spawning stock biomass}$, the estimated reference point was the same as the stochastic projection. On the basis of these results, I recommend calculating the reference point based on a stochastic projection for which the mean of the simulated growth rates is used. A reference point based on a %MSP approach using the $\Sigma \text{recruits} / \Sigma \text{spawning stock biomass}$ results in an equivalent estimate of the reference point but does not convey important information on the expected population growth rate at higher or lower rates of fishing mortality.

A biological reference point based on the Leslie matrix

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Advice to fishery managers on desirable harvest or exploitation rates is ideally based on full knowledge of fishery dynamics, including information on the fish population's stock-recruitment relationship, growth and maturation schedule, and bioeconomic considerations. With a lack of such complete information, guidance to fishery managers often takes the form of providing an estimate of fishing mortality and a comparison of that rate to one or more biological reference points (e.g. Clark, 1991; Anonymous¹). Numerous biological reference points exist, each concerned with a somewhat different aspect of population response to harvesting. One class of reference points focuses on yield per recruit as a function of fishing mortality. The general goal of this class of reference points is to optimize harvest rates in relation to natural mortality and growth (i.e. prevent growth overfishing; Beverton and Holt, 1957). For example, F_{max} is the fishing mortality rate at which yield per recruit is maximized (Beverton and Holt, 1957). A related reference point is $F_{0.1}$, which is the fishing mortality rate where the slope of the yield per recruit curve is 10% of the slope at the origin (Gulland and Boerema, 1973). Fishing at F_{max} or $F_{0.1}$ results in maximal or nearly maximal yield from a fishery when recruitment is independent of stock size. A limitation of this class of reference points, however, is that reductions in recruitment are often evi-

dent when stocks are depleted to low levels (e.g. Overholtz et al., 1986). Thus, management advice based on F_{max} or $F_{0.1}$ can result in declines in abundance through recruitment overfishing (Sissenwine and Shepherd, 1987), ultimately resulting in reduced total yield from a stock.

As a counterpart to reference points based on yield per recruit, several reference points based on stock-recruitment considerations have been developed. The goal of these reference points is to provide a measure of fishing mortality that will likely avoid recruitment overfishing. An example of this type of reference point is F_{med} which is based on the median of the observed levels of recruits produced per unit of spawning stock biomass (R/SSB) (Sissenwine and Shepherd, 1987). The rationale behind this reference point is that fish abundance is maintained when the spawning stock biomass produced by a cohort over its lifetime is equal to the spawning stock biomass of the parent population when the cohort was spawned. Related to F_{med} is a set of reference points based on the spawning stock biomass per recruit (SSB/R) in relation to the SSB/R that would be produced if the

¹Anonymous. 1996. Report of the 20th Northeast Regional Stock Assessment Workshop (20th SAW): SAW Public Review Workshop. Northeast Fisheries Science Center Reference Document 95-19. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Woods Hole, MA, 52 p.

stock were not fished (Gabriel et al., 1989; Clark, 1991). These reference points are termed percent maximum spawning potential (%MSP) or spawning per recruit (SPR) reference points. As an example, Gabriel et al. (1989) found that fishing at F_{med} for Georges Bank haddock results in a SSB/R ratio of about 30% ($F_{30\%}$) of the SSB/R that would be produced if the stock were not fished.

There are several limitations to this group of reference points. First, the population-level effect of fishing above or below a given reference point is not immediately obvious. For example, if fishing at $F_{30\%}$ results in a stable population, the rate of population decline when fishing mortality results in a 20% MSP is not clear. Secondly, although the use of the median SSB/R is an attempt to determine the SSB/R ratio with a robust estimator, the effects of variability in recruitment have not been closely examined in the estimation process. There is also an implication that two fishing mortality patterns (i.e. combination of fishing intensity and age at entry into the fishery) that produce the same SSB/R will result in equivalent impacts on the population. To my knowledge, this implication has not been investigated. Finally, these reference points treat the R/SSB ratio as being independent of stock size. Although the stock-recruitment relationship for many stocks is so weak and highly variable that this is a reasonable approach (Clark, 1991), this assumption should be examined on a case-by-case basis.

The goal of this paper is to explore a method for computing a reference point based on stock-recruitment data that overcomes some of the limitations of F_{med} and related reference points concerned with recruitment overfishing. In particular, this method allows for 1) a direct determination of the population-level impact of fishing above or below the reference point and, 2) incorporation of information on recruitment variability into the estimated reference point. This method does not, however, take into account any curvature in the stock-recruitment relationship (i.e. this method assumes that recruitment is proportional to spawning stock biomass). Although this assumption is not always met, the reduction in abundance that occurs for most exploited fish stocks results in a reduced magnitude of density-dependent effects on recruitment. Thus, the use of this reference point is likely to be reasonable for fish stocks that have already been exploited (Francis, 1997).

Methods

The proposed method is founded on an eigenvalue analysis of Leslie matrices representing the population's dynamics under exploitation. As such, the model

is specifically intended for use for fish with a single breeding season per year. The underlying model is based on one developed by Quinn and Szarzi (1993), which led to determination of the fishing mortality (F_{st}) that resulted in a stationary population in a Leslie matrix setting. Their results are extended by examining the effects of recruitment variability on the reference point and the relationship between this method and %MSP methods. This model is conceptually similar to those used for environmental impact assessment of power plants (e.g. DeAngelis et al., 1977; Cohen et al., 1983; Goodyear and Christensen, 1984) but differs in that it focuses on sustainable harvest rates across several age classes, whereas environmental impact assessment models typically focus on mortality of early life stages. Related methods have also been presented by Getz and Haight (1989). Their methods, however, are not explicitly framed toward providing a reference point for a fishery. Further, their methods are based on catch (in numbers or weight) whereas my methods are based on fishing mortality rates.

Developing a Leslie matrix representation of harvesting: deterministic case

Consider initially a population with no harvest, and where abundance estimates are available on an annual basis at the time of breeding. If we assume that the vital rates (i.e. age-specific reproduction and survival) are constant, the dynamics of the population can be represented by a Leslie matrix L_u ; (see Table 1 for a list of symbols and their definitions):

$$L_u = \begin{array}{|ccccc|} \hline E(0) & E(1) & E(2) & \dots & E(s) \\ S(0) & 0 & 0 & \dots & 0 \\ 0 & S(1) & 0 & \dots & 0 \\ 0 & 0 & S(2) & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & S(s-1) & 0 \\ \hline \end{array}$$

where $E(i)$ is age-specific fecundity, $S(i)$ is the annual survival rate from age i to $i+1$ and s is the maximum age. With this projection matrix, the population at time $t+1$ can be determined from the population at time t by the equation:

$$N_{t+1} = L_u N_t.$$

Note that estimates of natural mortality rate are also necessary to compute the previously mentioned reference points and are typically available for species where quantitative stock assessments are performed. Also note that although age-specific fecundity is not always measured in fish stock assessments, spawning stock biomass is commonly used as a surrogate

Table 1

Symbols used and their definitions.

	Definition
$E(i)$	Fecundity at age i .
$F(i)$	Instantaneous fishing mortality rate from age i to $i+1$.
F	Fishing mortality rate on fully recruited age class(es).
F_{st}	Sustainable fishing mortality rate on fully recruited age class(es).
L_e	Leslie matrix representing exploited population.
L_u	Leslie matrix representing unexploited population.
λ_e	Dominant eigenvalue of L_e .
λ_u	Dominant eigenvalue of L_u .
$M(i)$	Instantaneous natural mortality rate from age i to $i+1$.
$N(i)$	Number at age i .
N_t	Total population size at time t .
i	Age index.
$PM(i)$	Proportion of females mature at age i .
R/SSB	Recruits per unit of spawning stock biomass.
SSB	Spawning stock biomass.
SSB/R	Spawning stock biomass per recruit
s	Maximum age.
$S(i)$	Annual survival rate from age i to $i+1$.
t_c	Age at recruitment when vulnerability to the fishery is knife-edge.
$W(i)$	Weight at age i .
$X(i)$	Fecundity equivalents for fish of age i .

(see Rothschild and Fogarty (1989) for cautions on this practice, however). Because data on spawning stock biomass are more commonly presented in fishery assessments than data on fecundity, I will present the model using age-specific fecundity equivalents (i.e. spawning biomass of individual fish) rather than fecundity. In this representation, the survival rate of age-0 fish is expressed as recruits per unit of spawning stock biomass (R/SSB) rather than as actual survival rate from egg to age 1, and SSB is used in place of egg production. It is easily shown that the use of R/SSB and SSB in the Leslie matrix is algebraically equivalent to using fecundity and survival from egg to age 1.

Given the mapping of the vital rates [$E(i)$, $S(i)$] of the unexploited population into a Leslie matrix, it is straightforward to represent the dynamics of the population under exploitation. Observe that for the unexploited population $S(i)=e^{-M(i)}$, where $M(i)$ is the instantaneous natural mortality rate. For an exploited

population, $S(i)=e^{-(M(i)+F(i))}$ where $F(i)$ is the age-specific instantaneous rate of fishing mortality. The Leslie matrix for the population under exploitation (L_e) is thus formed in exactly the same manner as for the unexploited population except that annual survival rates are decreased through fishing mortality.

It is important to emphasize that in this analysis, fecundity and natural mortality (including age-0 survival or R/SSB) are assumed to be constant. As such, the determination of a reference point based on an analysis of L_e is valid over the range of stock sizes for which these age-specific fecundity and mortality rates apply.

Methods of analyzing the Leslie matrix are well established (e.g. Keyfitz, 1977; Caswell, 1989). Properties of the Leslie matrix under certain regularity conditions include the following:

- 1 The Leslie matrix has at least one positive root (eigenvalue);
- 2 The largest of these roots (the dominant eigenvalue or λ) determines the population growth rate, except in cases where the population is inherently cyclical and the largest roots are of equal magnitude;
- 3 If $\lambda > 1$ the population will increase;
If $\lambda = 1$ the population will remain steady;
If $\lambda < 1$ the population will decrease.

(Pielou, 1974; Caswell, 1989; Getz and Haight, 1989). Of particular importance to this reference point is the dominant eigenvalue which, in the deterministic case, is sufficient to determine the long-term trend in population abundance (Keyfitz, 1977; Cohen et al., 1983). Given these properties, the following assertion for the deterministic case can be made:

- 1 A population under exploitation can maintain itself at or above a given level of abundance only if the dominant eigenvalue of L_e (i.e. λ_e) ≥ 1 .

From this assertion arises the proposed reference point: F_{st} (for F steady, after Quinn and Szarzi, 1993) is a fishing mortality pattern where $\lambda_e = 1$. Note that F_{st} is actually a vector comprising two components: an overall level of fishing mortality (often termed fully recruited F) and the relative fishing mortality between age classes (often referred to as the partial recruitment vector or selection pattern), and that $F_i =$ (fully recruited F) \times (selection on age i). By convention, I will use the fully recruited F as an index of the overall level of fishing mortality, but stress that specification of the partial recruitment function is also necessary to determine the impact of harvesting on a population. Also note that there is an infinite set of fishing mortality patterns for which the condition that $\lambda_e=1$ is satisfied. For a given partial recruitment func-

tion, however, only one level of fishing will satisfy this condition. Note that the converse is not true; for a given level of fully recruited fishing mortality, numerous partial recruitment functions can satisfy the above condition. Because of the nature of these relationships, I will focus on those situations where the partial recruitment function is specified and solve for the level of fishing that is sustainable. Once the selection pattern and fully recruited fishing mortality are set, λ_c can be found by the power method as described by Johnson and Riess (1981).

Example of maintenance fishing mortality: deterministic case

Data from Georges Bank haddock (*Melanogrammus aeglefinus*) are used to illustrate the computation and application of this reference point. For ease of discussion, I first present general results assuming knife-edge recruitment to the fishery at age t_c with full vulnerability thereafter.

Age-specific fecundity equivalents ($X(i)$; Table 2) were computed as

$$X(i) = W(i) \times PM(i),$$

where $W(i)$ = mean weight (kg) at age i ; and

$PM(i)$ = proportion of females mature at age i .

and spawning stock biomass was computed as the product of fecundity equivalents and number of fish at age. Mean weight at age ($W(i)$) and proportion of females mature ($PM(i)$) reported by O'Brien and Brown² were used in this analysis. The instantaneous natural mortality rate ($M(i)$) of haddock age 1 and older is 0.2 (Clark et al., 1982), and a maximum age of 15 was used following Gabriel et al. (1989).

I computed annual R/SSB (Table 3) from the ratio of number of female fish at age 1 to their parental female spawning stock biomass (Clark et al., 1982; O'Brien and Brown²; Hayes and Buxton³) for the period 1931–94. For the entire data series, R/SSB averaged 0.5902. As noted by Gabriel et al. (1989), however, the R/SSB ratio (reflecting age-0 survival) appears to have declined following the collapse of the Georges Bank haddock stock during the early 1960s.

² O'Brien, L., and R. W. Brown. 1996. Assessment of the Georges Bank haddock stock for 1994. Northeast Fisheries Science Center Reference Document 95-13. National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA. 107 p.

³ Hayes, D. B., and N. G. Buxton. 1991. Assessment of the Georges Bank haddock stock. Papers of the Northeast Regional Stock Assessment Workshop, Research Document SAW13/1, 126 p.

Table 2

Age-specific characteristics of Georges Bank haddock. Fecundity equivalents (i.e. spawning biomass per individual) are denoted as X , instantaneous natural mortality rate as M , and partial recruitment as PR . The proportion mature and mean weights at age are from O'Brien and Brown (see Footnote 2 in the main text).

Age	Proportion mature	Mean weight (kg)	X	M	PR
0	0.00	—	0.000	—	0.00
1	0.08	0.486	0.039	0.2	0.00
2	0.46	0.676	0.311	0.2	0.07
3	0.88	1.197	1.053	0.2	0.65
4	1.00	1.621	1.621	0.2	1.00
5	1.00	2.021	2.021	0.2	1.00
6	1.00	2.424	2.424	0.2	1.00
7	1.00	2.780	2.780	0.2	1.00
8	1.00	3.192 ¹	3.192	0.2	1.00
9	1.00	3.548 ¹	3.548	0.2	1.00
10	1.00	3.924 ¹	3.924	0.2	1.00
11	1.00	4.297 ¹	4.297	0.2	1.00
12	1.00	4.667 ¹	4.667	0.2	1.00
13	1.00	5.034 ¹	5.034	0.2	1.00
14	1.00	5.398 ¹	5.398	0.2	1.00
15	1.00	5.758 ¹	5.758	0.2	1.00

¹ Predicted from von Bertalanffy growth equation fitted to observed data for ages 1 to 7.

At present the causes of the decline in the R/SSB ratio are not known. Several hypotheses explaining the observed decline in R/SSB have been put forth, including compensatory mortality on age-0 haddock (Collie and Spencer, 1993), changes in oceanographic conditions (Myers and Pepin, 1994), and increased predation or competition with elasmobranchs (Collie and Spencer, 1993). Although the cause is not known, a crucial consideration is the choice of an appropriate time period where R/SSB is representative of current population abundance and biomass and current environmental conditions.

One strategy to obtain a mean R/SSB value representative of "current" conditions is to average R/SSB from the most recent data point back several years. The philosophy behind this strategy is to smooth annual variations in R/SSB by averaging over a sufficiently long time period. The problem, however, is to define a time period sufficiently long to achieve adequate precision without introducing excessive bias. Averages over short time periods suffer from low precision and can vary considerably because of annual variation in R/SSB. If averages are taken over a time period spanning a wide range of population levels or

Table 3

Stock-recruitment data for Georges Bank haddock, 1931 to 1990. Data for 1931 to 1962 Hayes and Buxton (see Footnote 3 in the main text), and from 1963 to 1994 from O'Brien and Brown (see Footnote 2 in the main text).

Year	Spawning stock biomass (t) females only	Number of age-1 females produced (millions)	R/SSB	Year	Spawning stock biomass (t) females only	Number of age-1 females produced (millions)	R/SSB
1931	75,767	22.793	0.3008	1963	82,128	235.939	2.8728
1932	61,586	26.052	0.4230	1964	64,278	16.577	0.2579
1933	52,643	30.239	0.5744	1965	72,512	2.013	0.0278
1934	47,187	29.436	0.6238	1966	90,260	6.426	0.0712
1935	52,104	29.323	0.5628	1967	56,051	0.211	0.0038
1936	54,967	53.173	0.9674	1968	37,546	0.494	0.0132
1937	52,872	39.626	0.7495	1969	25,589	2.330	0.0911
1938	60,434	29.875	0.4943	1970	19,255	0.184	
1939	70,067	55.903	0.7979	1972	13,456	9.707	0.7214
1940	67,418	57.052	0.8462	1973	6,135	5.270	0.8590
1941	76,187	30.731	0.4034	1974	10,906	3.827	0.3509
1942	77,248	11.783	0.1525	1975	9,190	51.616	5.6165
1943	75,511	32.411	0.4292	1976	11,031	6.891	0.6247
1944	68,957	20.806	0.3017	1977	20,717	3.029	0.1462
1945	62,785	46.548	0.7414	1978	34,427	41.941	1.2183
1946	65,712	30.486	0.4639	1979	33,841	5.052	0.1493
1947	57,269	16.676	0.2912	1980	31,703	3.600	0.1136
1948	55,659	62.918	1.1304	1981	27,757	1.230	0.0443
1949	45,791	29.447	0.6431	1982	22,682	1.519	0.0670
1950	55,919	52.810	0.9444	1983	17,531	8.548	0.4876
1951	54,039	21.795	0.4033	1984	12,583	0.865	0.0687
1952	55,497	66.748	1.2027	1985	10,313	7.233	0.7013
1953	54,772	26.276	0.4797	1986	10,186	0.882	0.0866
1954	65,764	46.429	0.7060	1987	9,540	8.024	0.8411
1955	68,949	30.534	0.4428	1988	8,781	0.580	0.0661
1956	78,979	31.155	0.3945	1989	9,061	1.244	0.1373
1957	75,364	29.630	0.3932	1990	9,762	0.991	0.1015
1958	75,995	63.270	0.8326	1991	8,682	4.125	0.4751
1959	77,394	61.685	0.7970	1992	6,231	7.219	1.1586
1960	93,667	26.950	0.2877	1993	5,001	3.754	0.7507
1961	113,366	19.368	0.1708	1994	7,324	3.938	0.5377
1962	109,001	95.348	0.8747				

spanning a trend in environmental conditions, the estimate of future R/SSB may be biased. For this stock, mean R/SSB for periods of 5 to 15 years appear relatively stable. Over longer periods of time, mean R/SSB shows an upward trend, punctuated by sharp increases corresponding to the 1963 and 1975 year classes when R/SSB ratios were much higher than in any other years. Because of the trends observed over longer periods of time, I chose the time period from 1976 to 1994 as representative of “current” conditions for R/SSB, or equivalently, age-0 survival. For this time period, R/SSB averaged 0.4092, and had a median of 0.1493.

Based on the mean R/SSB for 1976 to 1994, the haddock population would be expected to grow at a rate

of 18.0% per year with no exploitation (i.e. $\lambda_u=1.180$). For knife-edge recruitment, I computed λ_e for fishing mortality rates ranging from 0 to 2.0 (Fig. 1) and for ages at entry (t_c) from 1 to 5 years and for the commercial fishery age selectivity observed in 1993–94 (Table 2). Additionally, I determined F_{st} and %MSP (following the methods of Gabriel et al., 1989) for each age at entry (Table 4). It is apparent from this analysis that as age at entry is delayed, the impact of fishing on the population is decreased (Fig. 1). Thus, higher fishing mortality rates can be sustained when recruitment to the fishery is delayed (Table 4). In fact, when the age at entry is 5 or greater, any level of fishing mortality is sustainable.

These conclusions are not new; analysis of SSB/R yields similar insights into the response of populations

to harvesting. The analysis of the Leslie matrix offers information not available in the analysis of SSB/R, however. First, the consequences of overfishing or “underfishing” are clearly evident from the graph of λ_e against fishing mortality rate. For example, for an age at entry of 3 years, F_{st} is 0.465. If the fishing mortality rate was limited to 0.20 (for example), the population would be expected to increase at a rate of about 8.8% per year (Fig. 1). Likewise if fishing mortality was increased to 1.0, the population would be expected to decline at a rate of about 10.3% per year (Fig. 1).

When %MSP is plotted against lambda resulting from various levels of fishing mortality and ages at entry into the fishery, it is apparent that equal %MSP values are obtained for the same lambda only at two points along each of the curves. The first point is for the unfished population when lambda is at a maximum and there is 100% MSP. The second point where all %MSP values are equal is when lambda is equal to 1.00 (Fig. 2). These results demonstrate the assertion that fishing mortality rates that result in equal %MSP values do not necessarily result in the same population dynamics (i.e. the same rate of increase or decrease). The reason for this disparity is that in a growing or declining population, the timing of reproduction during the lifetime is important, as well as the total lifetime egg production. For example, when a population is growing, earlier realization of lifetime spawning potential contributes more to population growth than later reproduction. This relationship is evident when the formula for lifetime spawning stock biomass (on which %MSP is based) is compared to the formula for reproductive value, upon which the rate of population change depends. Observe that lifetime spawning stock biomass per newborn individual is (Gabriel et al., 1989)

$$SSB/N_0 = S(0)W(1)PM(1) + S(0)S(1)W(2)PM(2) + S(0)S(1)S(2)W(3)PM(3) + \dots$$

This formula is equivalent to that for the “net reproductive rate” (Caswell, 1989) which is the expected number of offspring produced by a newborn over its lifetime. With the above notation, the reproductive value (Caswell, 1989) of an age-1 individual can be expressed as

$$\text{Reproductive value} = \frac{S(0)S(1)W(2)PM(2)\lambda^{-1} + S(0)S(1)S(2)W(3)PM(3)\lambda^{-2} + S(0)S(1)S(2)S(3)W(4)PM(4)\lambda^{-3} + \dots}{\lambda - 1}$$

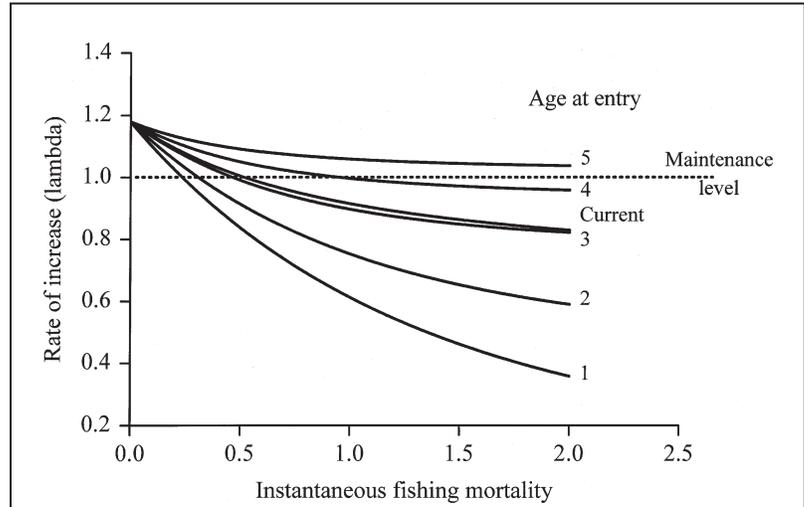


Figure 1
Rate of population increase (lambda) in relation to instantaneous fishing mortality (F) for a range of age at entry into the fishery.

t_c	F_{st}	%MSP
1	0.236	27.20
2	0.309	27.20
3	0.465	27.20
Current	0.519	27.20
4	0.956	27.20
5	>2.0	—

These formulae are similar except for the addition of the term λ^{-i} , where i is the age index. Classical demographic theory shows that the growth rate of a population is dependent on the reproductive value rather than on the net reproductive rate (Caswell, 1989). These two quantities are clearly related, however.

Currently, Georges Bank haddock become vulnerable to the fishery at age 2 but are not fully recruited until age 4 (Table 2). With this partial recruitment vector, F_{st} is 0.519. The graph of λ_e against F (Fig. 1) indicates that if F is held at its 1994 value of about 0.29, the population would be expected to increase at a rate of 6.35% per year. If F is reduced to 0, the stock would be expected to increase at a rate of 18.0% per year. The expected rate of increase when F is below F_{st} is particularly pertinent to cases where stock rebuilding is desired because this analysis allows the de-

termination of how rapidly the stock will be rebuilt under various levels of fishing mortality.

Developing a Leslie matrix representation of harvesting: stochastic case

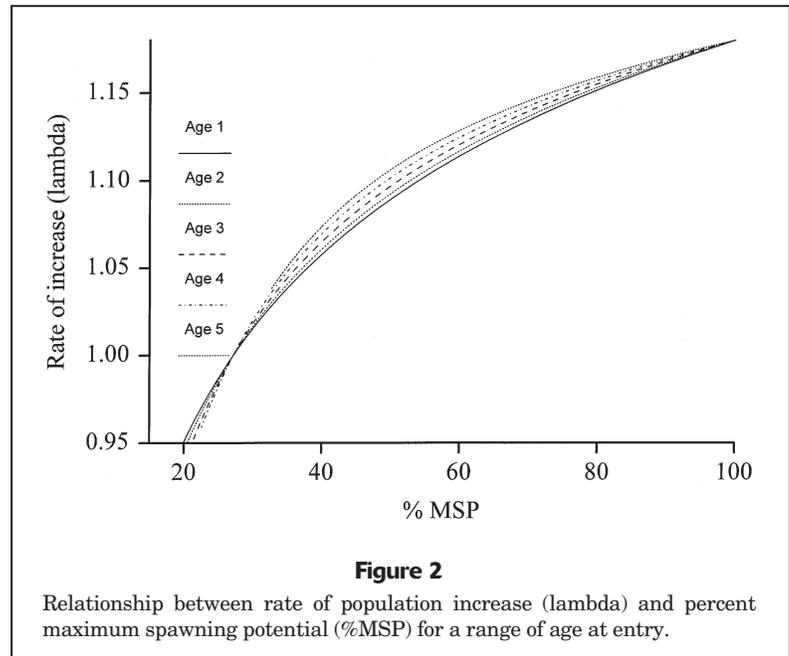
One of the major challenges facing fishery managers is to determine appropriate reference points for fish populations that show variable recruitment. When one or more elements of the Leslie matrix vary in a stochastic fashion, no general closed-form expressions for the growth rate of the population are available (Tuljapurkar, 1989). Results of theoretical studies of stochastic Leslie matrices are useful, however, in guiding the analysis and interpretation of matrices with entries that vary over time. Two results summarized by Tuljapurkar (1989) that are particularly useful in this analysis are

- 1 The analog to λ for deterministic matrices is the mean population growth rate, in contrast to the growth rate of the average population. This is equivalent to the mean rate of change in the logarithm of population size (N).
- 2 The distribution of projected population size (N) over time tends towards a lognormal distribution when the dynamics are governed by a stochastic matrix.

From these results, maintenance fishing mortality can be defined as the fishing mortality that results in an average population growth rate of 0 (equivalent to $\lambda_e=1$). Because this measure is analogous to λ , I will use the symbol λ for its representation but emphasize that computationally the measures for deterministic and stochastic Leslie matrices differ. An important corollary of the above two results is

- 3 A population growing deterministically at the mean growth rate does not produce the mean of the population sizes produced in the stochastic representation. Nor does a deterministic matrix composed of the means of the stochastic matrices produce a population with the same dynamics as applying the stochastic matrices.

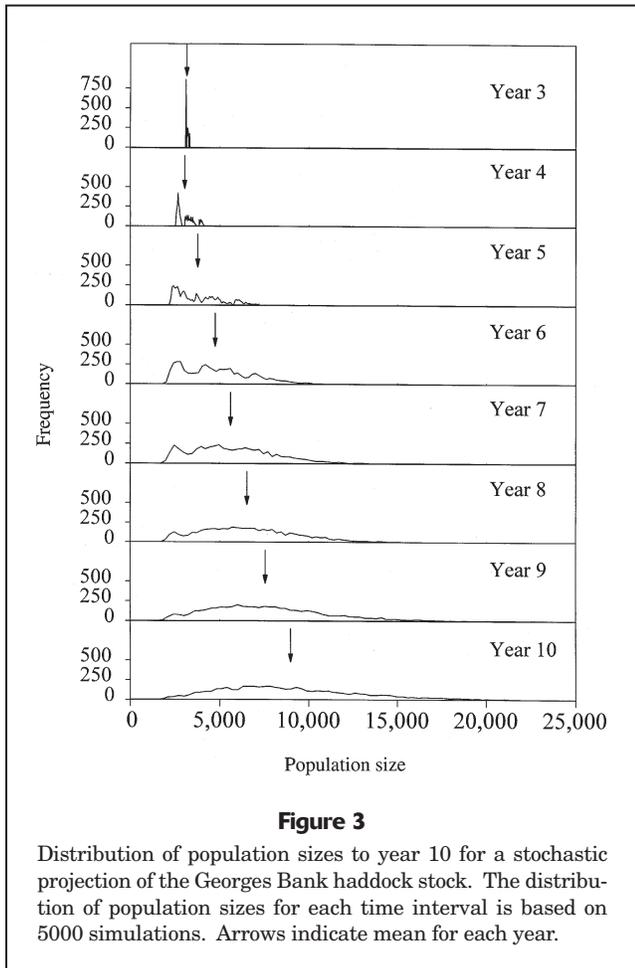
To illustrate these theoretical results, I performed a simulation of the Georges Bank haddock stock dynamics using a stochastic Leslie matrix. In this case, I focused on the effects of stochastic age-0 survival as represented by R/SSB. I performed this simulation



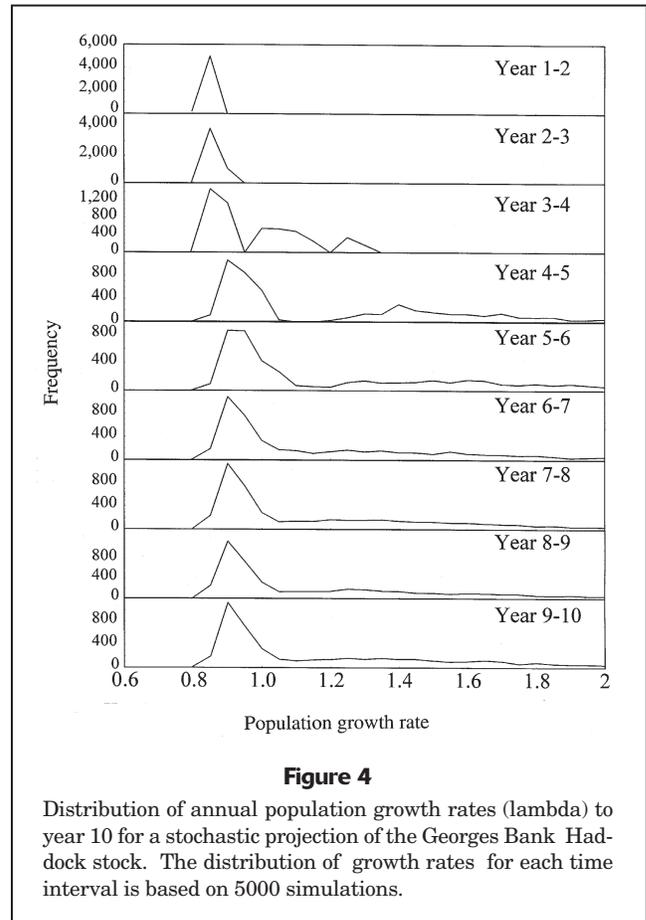
by projecting a starting population forward in time, with the value for R/SSB for each year selected with equal probability from observed values from 1976 to 1994. Five thousand replicates were simulated for a 150-year period.

Results of these simulations are in accord with the theoretical assertion that N_t is distributed lognormally; for times greater than 110 years, the $\ln(N_t)$ did not differ significantly from a normal distribution at $\alpha=0.05$. It is interesting to note that N_t is lognormally distributed, even though the stochastic element (R/SSB) was not normally or lognormally distributed itself. The lognormal distribution of N_t arises from the fact that N_t is the result of the process of sequential multiplications of random elements (Aitchison and Brown, 1976). When the distribution of population size is plotted over time (Fig. 3), it is clear that the variance increases rapidly. When year-to-year population growth rates (i.e. N_{t+1}/N_t) are computed for individual simulation results, the distribution of growth rates shows an initial transient response for the first 5 years but thereafter settles into a stable distribution from year to year (Fig. 4). Because of the transient dynamics, I began the evaluation of long-term dynamics with year 10.

One of the critical theoretical results is that the growth rate of a population governed by stochastic rates tends towards a single value in the long run. This is what Tuljapurkar (1989) terms the "almost sure population growth rate." When the growth rate is computed over progressively longer intervals, the distribution shows a convergence on nearly the same



mean value (Table 5) with a decreasing variance (Fig. 5). This result has both theoretical and pragmatic implications. Of theoretical importance is the concept that although the variance of projected population abundance increases over time, the variance of the growth rates declines over time. Thus mean population growth rate can be used in defining a maintenance fishing mortality rate. The practical consequence of the above result is that at least two different strategies can be used to compute λ for a stochastic population. One strategy is to project the population for a long period of time (e.g. hundreds of years) to make a precise estimate of the long-term population growth rate. This strategy makes use of the fact that the variance of the long-term population growth declines as the period of projection is lengthened. A problem with this approach, however, is that for projections over a long period of time, population abundance can become so large or small that it cannot be directly represented on a digital computer, causing a numeric overflow or underflow. A preferable strategy is to compute λ for a large number of simulations over a shorter



time period (e.g. 150 years). This method avoids the problem of numeric overflow and achieves precision in the estimate of mean λ by having a large number of simulations.

Based on the current partial recruitment vector to the fishery, a fishing mortality of 0.450 (F_{st}) would result in an average population growth rate of zero (Table 6). The fishing mortality that results in a zero growth rate for the mean population size was higher, at 0.517 (Table 6). Interestingly, this is nearly the same as F_{st} computed for the deterministic case by using the mean R/SSB. The estimate of F_{med} with these same data is much lower than F_{st} —only 0.069 (Table 6). When a deterministic Leslie matrix analysis was made with the corresponding median R/SSB, it resulted in an estimate of F_{st} that was nearly the same as F_{med} (Table 6). This finding illustrates the basic connection between these methods when they are operating on the same inputs. As an additional comparison, I computed SSB/R as the ratio $\Sigma SSB / \Sigma R$ instead of the mean (or median) of the individual year ratios. This method is based on sampling theory that suggests that the ratio of the sums is a less biased estima-

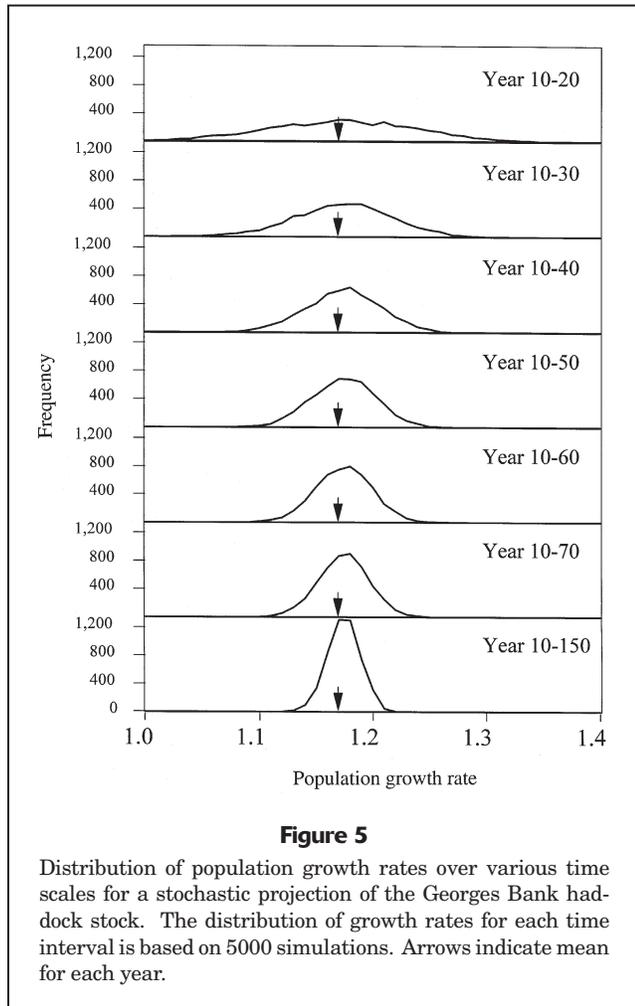


Table 5
 Mean and coefficient of variation (CV) of 5000 simulations of long run population growth rate for Georges Bank Haddock without fishing.

Time interval	Mean	CV
Year 10–20	0.1552	37.02
Year 10–30	0.1555	23.28
Year 10–40	0.1558	18.03
Year 10–50	0.1559	15.23
Year 10–60	0.1559	13.34
Year 10–70	0.1560	12.07
Year 10–150	0.1563	7.60

Table 6
 Comparison of F_{st} with deterministic analyses, stochastic analyses, and with %MSP calculations.

Type of simulation	Recruitment input	F_{st}
Deterministic	Mean R/SSB	0.519
Deterministic	Median R/SSB	0.070
Stochastic (mean of rates)	Uniform probability	0.450
Stochastic (mean of populations)	Uniform probability	0.517
%MSP	Mean SSB/R	0.519
%MSP	Median SSB/R	0.069
%MSP	$SSB/R = \Sigma SSB / \Sigma R$	0.449

tor of the “true” ratio than is the mean of the individual ratios (e.g. Cochran, 1977). The value for SSB/R obtained with this method was 2.685, and when used in place of the median SSB/R in the F_{med} calculations, resulted in an estimated reference point of 0.449—essentially the same as in the stochastic simulation where the mean population growth rate was zero (Table 6).

Discussion

The primary purpose of this paper was to demonstrate how the Leslie matrix can be used to compute a reference point for harvested populations and to contrast this method with the SSB/R method currently in use. One of the major findings was that the SSB/R method and the Leslie matrix approach produce similar estimates of sustainable fishing mortality when they are based on the same inputs. This is not surprising given the similarity between reproductive value, on which the Leslie matrix is based, and lifetime spawn-

ing stock biomass per recruit which the SSB/R approach uses.

Although the two methods produce similar estimates of sustainable fishing mortality, the Leslie matrix approach is preferable because of the additional direct information it provides regarding the population response to fishing at levels different from the reference point. Furthermore, when population growth rate is different from zero, equal levels of SSB/R do not result in the same population growth rate for different partial recruitment vectors. These differences are small, however, in relation to changes in population growth rate owing to changes in fishing mortality.

Given the various approaches illustrated (e.g. deterministic vs. stochastic), the basic question is what method to use. On the basis of theoretical advances in the population dynamics literature and results presented here, I recommend the use of a stochastic analysis where the mean of the population growth rates is used as the “best” measure of growth for harvested populations. A stochastic analysis is preferable be-

cause it can fully represent the information contained in the distribution of observed R/SSB values. Also, a stochastic simulation can be used to provide a measure of the uncertainty associated with estimates of the biological reference point. The use of the mean population growth rates instead of the mean of the population sizes is justified on theoretical grounds (Tuljapurkar, 1989). As shown in Table 6, use of the mean R/SSB in a deterministic analysis or the rate of growth of the mean population size in a stochastic simulation tends to result in higher estimates of sustainable fishing mortality (or, alternatively, a higher estimate of population growth rate for a given fishing mortality rate) than does the stochastic simulation where the mean of population growth rates are used as the output. I feel that the reason for this difference hinges on the distinction between projections and forecasts (Caswell, 1989). If we view the long-term simulation results as forecasts, this implies that we could use the distribution of population size (and the mean of the distribution) as the best estimate of the future state of the population. In these simulations, however, the mean population size is strongly influenced by the very high values that occur in the right-hand tail of the lognormal distribution. These estimates are far above what has ever been observed for this stock, and are probably not biologically realistic. As such, they should not be treated as true forecasts of the future population. In contrast, if we view the analysis as a projection, the goal is not to forecast future population size but rather to use the results to determine the population growth rate that is represented by the current Leslie matrix. By knowing the current population growth rate, it is possible to find the fishing mortality rate that maintains an expected value for population growth of zero, which would result in a statistically stationary population.

In a stochastic setting, the entire distribution of R/SSB ratios is used to portray the reproductive success for the stock. When a deterministic analysis is desired, however, it is necessary to choose among several possible measures of central tendency for the R/SSB ratio. Sissenwine and Shepherd (1987) advocated the use of the median R/SSB ratio as a way of robustly portraying the reproductive success of a stock. Their rationale was that the frequency of relatively poorer recruitment is balanced by years of better recruitment when the median R/SSB is used. Table 6 illustrates, however, that using the median of the observed R/SSB ratios can result in estimates of sustainable fishing mortality that are substantially different from the stochastic simulations, which are arguably the best to represent the population's dynamics. The use of the mean of the observed R/SSB ratio as the measure of central tendency can likewise result in estimates

of sustainable fishing mortality that differ from the standard set by stochastic simulations. The primary reason for this difference is that use of a mean of the observed ratios is biased high in relation to the preferred estimator of the ratio (in this case the sum of recruitment over the sum of spawning stock biomass; Cochran, 1977). As such, the use of the mean of the observed R/SSB values can also be inaccurate. Among the measures presented here, the estimator $\Sigma \text{recruitment} / \Sigma \text{spawning stock biomass}$ should be used as the measure of central tendency for the R/SSB ratio in deterministic analyses. The use of this measure results in point estimates of sustainable fishing mortality that are essentially the same as a full stochastic analysis.

Although the Leslie matrix is a useful tool to portray the dynamics of harvested populations and to determine appropriate reference points, several issues arise that are of considerable practical importance. As alluded to earlier, a significant challenge is how to determine what is an appropriate distribution for the R/SSB ratio. Because of the variability in R/SSB over time and the occurrence of occasional large year classes, it is very difficult to determine what time frame is representative of the present. Although the answer to this question is beyond the scope of this paper, I feel that the best approach is to plot the mean R/SSB ratio over progressively longer time periods back from the present to determine if there are any temporal trends or epochs in the data set. The analyst should then use his or her judgment based on other biological information over time (such as stock size, mean weight per individual at age, and maturation schedule) to determine an appropriate period to use as the basis for stochastic simulations. It is important to emphasize that the dilemma of choosing a representative time period is not unique to analyses in which the Leslie matrix is used, and the same problem arises for computing any biological reference point.

In addition to the difficulty of determining what is a representative time period for the present population, a fundamental question is how to represent the dynamics of populations with a density-dependent stock-recruitment relationship. In principle, this can be approached by altering the R/SSB ratio as a function of stock size (e.g. Quinn and Szarzi, 1993). Although I agree with Quinn and Szarzi's (1993) approach, the challenge of accurately specifying the distribution of R/SSB ratios at different stock sizes is even greater than specifying the current distribution.

As a final comment, biological reference points for fish populations are not necessarily targets for fishery management (Mace, 1994), nor are they inviolate boundaries that may not be crossed. Rather, they are most useful as a means of comparing the consequences

of different choices among fishery management options. For example, it is appropriate to allow fishing mortality to exceed the biological reference point if the goal is to reduce an overly abundant fish stock. Likewise, they can be useful in projecting the likely growth of a population under more restrictive fishery management measures. In the end, however, they may be most useful as a reminder and a warning that there are limits to the productive capacity of fish population and that if we consistently exceed their limits, population declines are almost certain to occur (Francis, 1997; Myers, 1997).

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