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# Individual-based yield-per-recruit analysis, with an application to the Atlantic sea scallop, *Placopecten magellanicus*

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**Abstract:** There can be considerable variation in fishing mortality risk among individuals in a stock, especially for sedentary or sessile species. An individual-based per-recruit model is proposed that can systematically deal with variability in fishing mortality among recruits. These variations can alter the yield per recruit (YPR) and biomass per recruit (BPR) that would be predicted from conventional theory. Where the YPR curve is concave, standard theory will tend to overestimate YPR, whereas the opposite will be true where the YPR curve is convex. Additionally, variations in fishing mortality among individuals can create a mismatch between conventional metrics of mean fishing mortality and that required to properly apply standard per-recruit theory. The concept of "recruit-weighted" fishing mortality is introduced to deal with this problem. An application of the model to the Atlantic sea scallop, *Placopecten magellanicus*, is presented that demonstrates that standard per-recruit theory may often misrepresent true YPR and BPR.

**Resume:** Il peut y avoir une variation importante du risque de mortalité due à la pêche parmi les individus d'un même stock, particulièrement chez les espèces sédentaires ou sessiles. On trouvera ici une modélisation "par recrue", basée sur l'individu, qui permet de traiter de la variabilité de la mortalité due à la pêche chez les recrues. Ces variations peuvent affecter la prédiction du rendement et de la biomasse par recrue (BPR) par les théories habituelles. Lorsque la courbe de rendement par recrue (YPR) est concave, la théorie standard tendra à surestimer le rendement par recrue; elle le sous-estimera lorsque la courbe est convexe. De plus, les variations de la mortalité due à la pêche d'un individu et l'autre peuvent générer un désaccord entre les métriques conventionnelles de la mortalité moyenne due à la pêche et celles qui sont requises pour l'application correcte de la théorie standard "par recrue". L'introduction du concept d'une mortalité due à la pêche pondérée par recrue permet de résoudre ce problème. L'application du modèle au pétoncle géant, *Placopecten magellanicus*, démontre que la théorie standard peut souvent fausser les véritables valeurs de rendement et de biomasse par recrue.

[Traduit par la Rédaction]

## Introduction

One of the key assumptions of conventional yield-per-recruit (YPR) theory (Beverton and Holt 1957; Gulland 1983; Quinn and Deriso 1999) is that all individuals in a stock have the same growth rates and mortality risks, or at the very least, the expected yield obtained from recruits with the mean growth and mortality rates is representative of the yield obtained from averaging over all recruits in the fishery. For mobile species that are fairly "well mixed", this assumption may be a reasonable approximation. On the other hand, high variation of fishing mortality rates within sessile stocks may cause difficulties when applying standard YPR theory.

To take one simple example, suppose (average) fishing mortality is maintained at  $F_{max}$  the point where optimal YPR is obtained. Suppose further that one portion of the

stock is fished at a level  $F_J$  that is below  $F_{max}$  while the other is fished at a level  $F_2$  above  $F_{max}$  (see Fig. 1). The resulting average YPR that would be obtained in this case would clearly be less than that obtained if all recruits had the identical fishing mortality risk  $F_{max}$ , as would be assumed in conventional YPR theory.

The above example is a demonstration of a general mathematical result known as Jensen's inequality (see, e.g., Feller 1966; Ruel and Ayres 1999). In the present context, Jensen's inequality implies that if the fishing mortality risks of all recruits are less than the point of inflection  $c$  indicated in Fig. 1, so that they all lie in the region where the YPR curve is concave (down), then the YPR, when averaged over all recruits, is less than the yield of an "average" recruit that suffers the mean fishing mortality. In other words, in this situation, conventional YPR analysis would always overestimate the actual YPR that would be obtained when there is variation in individual fishing mortality risk. The degree of this overestimation depends on the amount of nonlinearity (i.e., the magnitude of the second derivative) of the YPR curve; it will be high where the nonlinearity is pronounced, and less substantial where the curve is nearly linear. If, instead, the fishing mortality risks of all recruits are larger than  $c$ , and so are in the region where the YPR curve is

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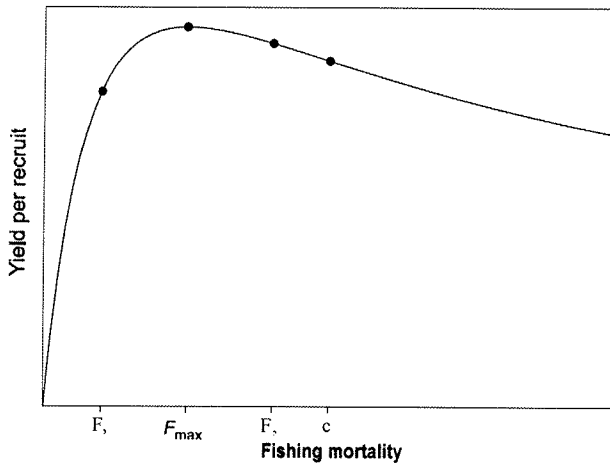
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Fig. 1. Yield-per-recruit (yPR) curve indicating the fishing mortality producing maximal yield ( $F_{max}$ ), example fishing mortalities  $F_1$  and  $F_2$  which average to  $F_{max}$  and the inflection point  $c$ . The yields produced by these four fishing mortalities are indicated by the circles on the graph.



convex, then Jensen's inequality implies that standard per-recruit theory would underestimate the mean YPR averaged over all recruits.

Variations of fishing mortality risks among individuals may also cause difficulties in the computation of wholestock fishing mortality rates. Fishing mortality (n-weighted) is typically computed as the number removed per unit time divided by the total population. If some part of the stock is fished less than average, then this subpopulation will be disproportionately overrepresented in the population as compared to the portion of recruits that came from this subpopulation. This causes a mismatch between the standard calculation of fishing mortality and per-recruit calculations because the estimated n-weighted fishing mortality will underestimate the mean fishing mortality when averaged over all recruits. This problem would be even more serious if biomass-weighted fishing mortalities were used.

To take a simple example, suppose a stock produces  $N_0$  recruits annually and has a natural mortality rate of  $M \sim 0.1$ . Suppose 90% of the recruitment occurs in an area where the fishing mortality on recruited individuals  $F_1 \sim 1.0$ , independent of age. At equilibrium, this subpopulation will have  $0.9N_0/(M + F_1)$  surviving members (Beverton and Holt 1957). The other 10% of the recruitment occurs in an area where the fishing mortality  $F_2 \sim 0.1$ , independent of age. This subpopulation will have  $0.1N_0/(M + F_2)$  surviving members at equilibrium. Thus, the proportion of the stock from the first subpopulation is

$$(1) \quad \frac{0.9/(M + F_1)}{0.9/(M + F_1) + 0.1/(M + F_2)} \sim 0.62$$

The n-weighted fishing mortality is therefore  $0.62(F_1) + 0.38(F_2) \sim 0.66$ . However, the mean fishing mortality when each recruit is given equal weight is much higher (0.91). Thus,  $F \sim 0.66$  is not the mean (i.e., expected) fishing mortality of a recruit, nor would the yield obtained by a conventional YPR calculation with  $F \sim 0.66$  represent the mean

yield obtained from a recruit. In this simple example, it would be possible to resolve these difficulties by dividing the stock into two parts, and calculating the correct fishing mortalities and YPR for each part. However, in more complex situations, such subdivision of stocks may be neither practical nor desirable.

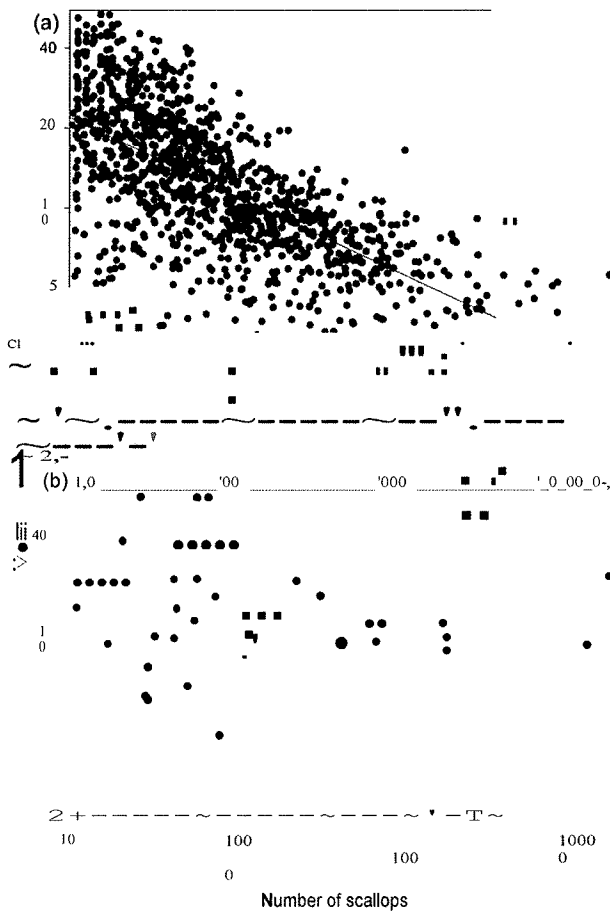
Variations in fishing mortality risk within a stock are likely to be common. Fishers attempt to maximize their profits by fishing in those areas where their net revenue per unit time is high, often leading to spatial variation in fishing mortality (Caddy 1975; Gillis et al. 1993; Holland and Sutinen 1999). In species where individuals do not readily move between heavily and lightly fished areas, the implicit assumption in per-recruit analysis that all individuals suffer similar levels of fishing mortality can be strongly violated.

A good example of this phenomenon can be seen in sea scallops, *Placopecten magellanicus*, on Georges Bank in the Northwest Atlantic. Annual scallop surveys of the U.S. portion of Georges Bank and surrounding areas have been made since 1982 (see Serchuk and Wigley 1986). The average sea scallop meat weight of each tow of this survey from 1982 to 1994 is plotted on the y axis in Fig. 2a, excluding tows where fewer than 10 scallops were caught. The x axis of this plot presents the number of scallops caught on the tow. A clear pattern is seen in which large scallops are often observed in areas of low density, whereas in areas of high density, the average scallop meat weight is much smaller, and is around the size at which scallops recruit to the fishery.

In December 1994, three large areas on or near Georges Bank were closed to trawling and scallop dredging (Murawski et al. 2000). Figure 2b is similar to Fig. 2a, except it shows tows from the closed areas in 1999 and 2000 (excluding the southern portion of closed area II, which was reopened to fishing in 1999), after these areas had been closed for a number of years. In contrast to Fig. 2a, no relationship is present in Fig. 2b between density and average size. This indicates that the strong trend of decreased average size in high-density areas seen in Fig. 2a was a result of fishing activity. Fishing effort tends to be concentrated in productive, high-density areas' thereby inducing higher fishing mortality there. Thus, scallops that settle in high-density areas are typically fished before they can grow to the sizes often seen in areas of low productivity or in areas closed to fishing.

It was already noted by Beverton and Holt (1957) that such spatial variation in fishing mortality can complicate the relationship between effort and fishing mortality, and between fishing mortality and yield, so that the use of standard fisheries theory in this situation may produce incorrect results. Caddy (1975) pointed out that this problem is especially severe for sedentary and sessile stocks, and standard per-recruit theory may misestimate the actual YPR. He used explicit spatial simulations to show that traditional models that use a dynamic pool assumption may misestimate the yield obtained from the sea-scallop fishery. Unfortunately, the ideas of this pioneering work have often not been incorporated into the management of sedentary stocks. Part of the problem is that ad hoc spatial simulations lack the simplicity of traditional fisheries models, and that they seem to depend on the exact assumptions about the spatial configuration of the resource in the model. Another spatially explicit YPR

Fig. 2. (a) Mean meat weight of sea scallops on the L.I.S. portion of Georges Bank on each tow of the annual NMFS sea scallop survey between 1982 and 1994, plotted as a function of the number caught in the tow (tows where fewer than 10 scallops were caught were excluded). The linear (log-log) best leastsquares fit to this data is also shown. (b) A similar plot, but of the tows conducted in 1999-2000 of areas on Georges Bank that had been closed to fishing since December 1994.



model for shellfish stocks was introduced by Murawski and Fogarty (1984), who focused on the effect of localized density-dependent growth and mortality on YPR.

Models that take into account individual variations within a population have become increasingly common in recent years (e.g., Huston et al. 1988; DeAngelis and Gross 1992). Such "individual-based" models have often shown that variations in life history parameters among individuals have important effects on population dynamics.

The purpose of this article is to present a general method of taking into account variations among individuals in fishing mortality in the context of YPR analysis. This individual-based modelling approach requires only a general assumption about variation of fishing mortality in the population, and can give the same type of fishing mortality and biomass reference points as traditional per-recruit approaches.

**Methods**

If the growth rates, natural mortality ( $M$ ), and fishing mortality ( $F$ ) are known for an individual recruit, the expected YPR  $Y(F)$  for

that recruit can be calculated as in conventional per-recruit analysis (e.g., Beverton and Holt 1957; Gulland 1983; Quinn and Deriso 1999). Note that in the context of computing individual YPR, mortality must be interpreted as a risk (i.e., a probability per unit time) rather than the usual interpretation as a rate, and individual YPR needs to be interpreted as an expected value.

Here, a length-based per-recruit model for sea scallops was used to calculate expected individual yields (NEFSC 2001), similar to the "generic per-recruit model" described in Quinn and Deriso (1999). von Bertalanffy growth coefficients for shell heights (lengths) were obtained from Serchuk et al. (1979).  $M$  was set at 0.1 (Merrill and Posgay 1964). Shell heights  $L$  were converted into meat weight (potential yield)  $W$  by a shell height to meat weight formula of the form

$$(2) \quad \ln(W) \sim a + b \ln(L)$$

The parameters  $a$  and  $b$  were selected as the best least-squares fit to shell height and meat weight data. For Georges Bank,  $a = -11.6038$  and  $b = 3.1221$ , whereas for the Mid-Atlantic Bight,  $a = -12.2484$  and  $b \sim 3.2641$  (NEFSC 2001). YPR and biomass per recruit (BPR) for individual recruits were then calculated by the formulas

$$(3) \quad Y(F) \sim \int_0^{\infty} F \delta(t) W(t) SF(t) dt$$

$$(4) \quad B(F) \sim \int_0^{\infty} W(t) SF(t) dt$$

where  $a_0$  is the age (in years) at which the scallop reaches 40-mm shell height,  $a(t) = a_0 + 30$ ,  $W(t)$  is the meat weight at age  $t$ ,  $\delta(t)$  is the selectivity at age  $t$ , and  $SF(t)$  is the fraction of the 40-mm recruits that survive to age  $t$ . The integrals were calculated numerically with a time step of 0.01 years.

In this article, the individual variations in fishing mortality risks is the only type of variability considered. The variation in fishing mortality can be described by a cumulative distribution function (CDF)  $C(F)$ , which gives the probability that a randomly chosen recruit will have a (fully recruited) fishing mortality risk of less than  $F$ . The expected YPR,  $Y$ , of a randomly chosen recruit is then given by

$$(5) \quad Y \sim \int_0^{\infty} Y(F) dC(F)$$

In the case where  $C(F)$  is differentiable, and so has a probability density function  $c(F) = C'(F)$ , then eq. 5 becomes

$$(6) \quad Y \sim \int_0^{\infty} Y(F) c(F) dF$$

Individual-based BPR can be modeled similarly. If an individual experiences a fishing mortality risk  $F$ , the (expected) BPR  $B(F)$  for this individual can be computed by conventional means. The expected BPR of a randomly chosen individual is

$$(7) \quad B \sim \int_0^{\infty} B(F) dC(F)$$

To apply this theory in practice, it is necessary to estimate the CDF  $C(F)$ . One estimation technique will be discussed here, using sea scallops as an example. Estimating  $C(F)$  requires calculating fishing mortality on a relatively fine spatial scale. Techniques that estimate fishing mortality from year-to-year variations in age classes are impractical on these spatial scales owing to the high variability of survey data. Because these techniques are based on differences between surveys in adjacent years, they tend to amplify the already high measurement error present at small spatial scales (Conte and de Boer 1980). Instead, fishing mortality was inferred by using 10-

cal size-structure information, employing the formula of Ssentongo and Larkin (1973). This formula calculates total mortality  $Z$  from a given size structure, assuming von Bertalanffy growth, with parameters  $L^{\infty}$ , and  $K$ , constant mortality and recruitment, and a constant total mortality rate for lengths greater than some length  $l_e$ . Assuming a large sample size, this formula is (Gulland 1983)

$$(8) \quad Z = \frac{K}{\bar{y} - y_c}$$

where  $y_c = \ln(1 - L/L^{\infty}) / K$ , and  $\bar{y}$  is the mean value over all individuals whose lengths  $l$  are greater than  $l_e$  of

$$(9) \quad Y \sim \ln(1 - L/L^{\infty})$$

In sea scallops, lengths are scallop shell heights, and knife-edge recruitment is assumed to occur at  $l_e = 80$  mm. Fishing mortality  $F$  was obtained by the formula  $F = Z - M$ , with  $M = 0.1$ . The Ssentongo and Larkin formula is less sensitive to measurement error than those techniques that difference year-to-year survey values.

The assumption of constant recruitment in the Ssentongo and Larkin formula is of course not even approximately correct. A large year class will cause this formula to overestimate fishing mortality when it is first recruited to the fishery, and then underestimate it in later years as the year class matures. So while this formula may not accurately measure fishing mortality for a single year, it would be expected to be a reasonably reliable estimator of fishing mortality when averaged over many years.

To check this idea, I ran Monte Carlo simulations where  $F$  was fixed but recruitment was varied lognormally, with the mean, variance, and autocorrelation of the simulated recruitment matching that of the observed 1982-1999 U.S. Georges Bank sea scallop recruitment time series. The mean of the Ssentongo and Larkin estimates over 4000 years was within 10% of the correct fishing mortality  $F$  over a broad range of input fishing mortalities, and the mean estimate over all runs with various fishing mortalities matched the mean input fishing mortality to within 4%. This indicates that variable recruitment causes this formula to have at most a small bias. The Ssentongo and Larkin estimates were then blocked into 13-year time segments and averaged. The means of the blocks had a standard deviation that ranged between 0.05 at low fishing mortalities up to about 0.15 at high fishing mortalities, about one fourth that of the standard deviation of the unaveraged annual estimates of  $Z$ . Thus, while recruitment events may make the Ssentongo and Larkin method unreliable for a single year, it should give a reasonable estimate of temporally averaged fishing mortality in an area when these estimates are averaged over a number of years. This formula is also not sensitive to the exact value of  $l_e$  (provided it is large enough to insure full gear selectivity); changing  $l_e$  from 80 mm to 90 mm affected the estimated values of  $Z$  in the simulations by less than 1 %.

Annual National Marine Fisheries Service (NMFS) surveys of sea scallops have been conducted in Georges Bank and in the MidAtlantic Bight for the last 20 years (see Serchuk and Wigley 1986 for a more full description). I focused on the years 1982-1994, during which time both survey design and management measures were stable. After 1994, many management changes were made including closed areas, effort controls, and gear restrictions. This period may therefore not be comparable to previous years, and was excluded from the analysis. The surveys were based on a random stratified design, with the surveyed area divided into a number of strata defined by depth and region.

Mean recruitment  $r$  (per tow) was calculated for each survey stratum  $i$  over the time period 1982-1994. Recruits were defined as those scallops between shell heights of 40 mm (the smallest size reliably detected in the survey) to those corresponding to an age one year older than a 40-mm scallop, as estimated by von Bertalanffy growth equations (69 mm in the Mid-Atlantic Bight

and 72 mm in Georges Bank). If the area of stratum  $i$  is  $a_i$ , then the probability that a recruit chosen randomly over that time period was in that stratum is

(10)

$$\text{where } p_i = \frac{a_i r_i}{\sum_j a_j r_j}$$

the summation is taken over all strata. Mean fishing mortality  $P_i$  was estimated in each stratum; over the 1982-1994 time period by

calculating fishing mortality for each year by the Ssentongo and Larkin formula and then averaging over the years in the time period. The CDF  $Co(F)$ , the probability that a randomly chosen recruit was subject to a fishing mortality less than  $F$  during that time period, can be estimated as

$$(11) \quad Co(F) \sim \sum_{\{j: F_j < F\}} P_j$$

This gives an estimate of the historic CDF, based on past fishing patterns. To perform per-recruit analysis, it is necessary to compute the YPR for a variety of (mean) fishing mortalities, not just the one observed historically. Here, I will make the simple assumption that changing the mean fishing mortality does not affect the variability in that mortality. In other words, if  $F_h$  represents the mean (recruit-weighted) historical fishing mortality, then the CDF  $Ci(F)$  for a different mean fishing mortality  $F_i$  is given by

$$(12) \quad Ci(F) \sim Co\left(\frac{F_i}{F_h}\right)$$

The above procedure for estimating the fishing mortality CDF neglects within-stratum and year-to-year variation in fishing mortality, and is thus likely to somewhat underestimate the true individual variability in fishing mortality. Further uncertainty may be introduced by the estimation of the fishing mortality CDFs. However, the method described above is still a reasonable first approximation, and is useful in demonstrating the error made when variability in fishing mortality is neglected.

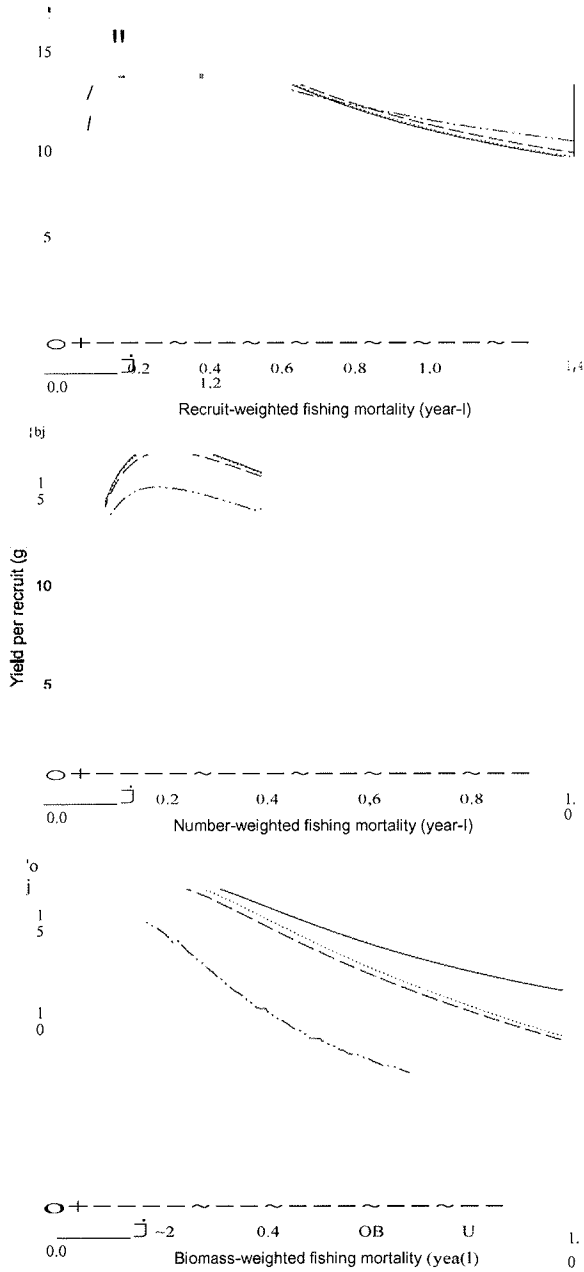
## Results

To explore the effect on YPR of variation of fishing mortality, YPR curves were computed (Fig. 3) from eq. 5 using a uniform probability distribution in which fishing mortality levels range by 0%, 25%, 50%, and 100% about the recruit-weighted mean fishing mortality  $F_0$  (i.e., fishing mortalities are distributed uniformly on the interval  $((1 - a)F_0, (1 + a)F_0)$ , where  $a \sim 0, 0.25, 0.5, 1$ , respectively). The  $x$  axis in Figs. 3a-3c represent recruit-weighted, number-weighted, and biomass-weighted fishing mortalities, respectively.

In all cases, individual deviations in fishing mortality risk tends to reduce YPR when the mean fishing mortality is near  $F_{max}$ , especially when variability is high. When recruit-weighted fishing mortalities are employed, variability in fishing mortality induces an increase in YPR at high fishing mortality rates. However, if biomass-weighted fishing mortalities are used, this variability causes considerable reductions in YPR at high fishing mortality rates. Results with number-weighted fishing mortalities fall between those employing recruit-weighted and biomass-weighted fishing mortalities.

Individual-based BPR curves are given in Fig. 4. Variation in fishing mortality causes the standard theory to underestimate actual recruit-weighted BPR. This is especially apparent at intermediate fishing mortality levels, where the

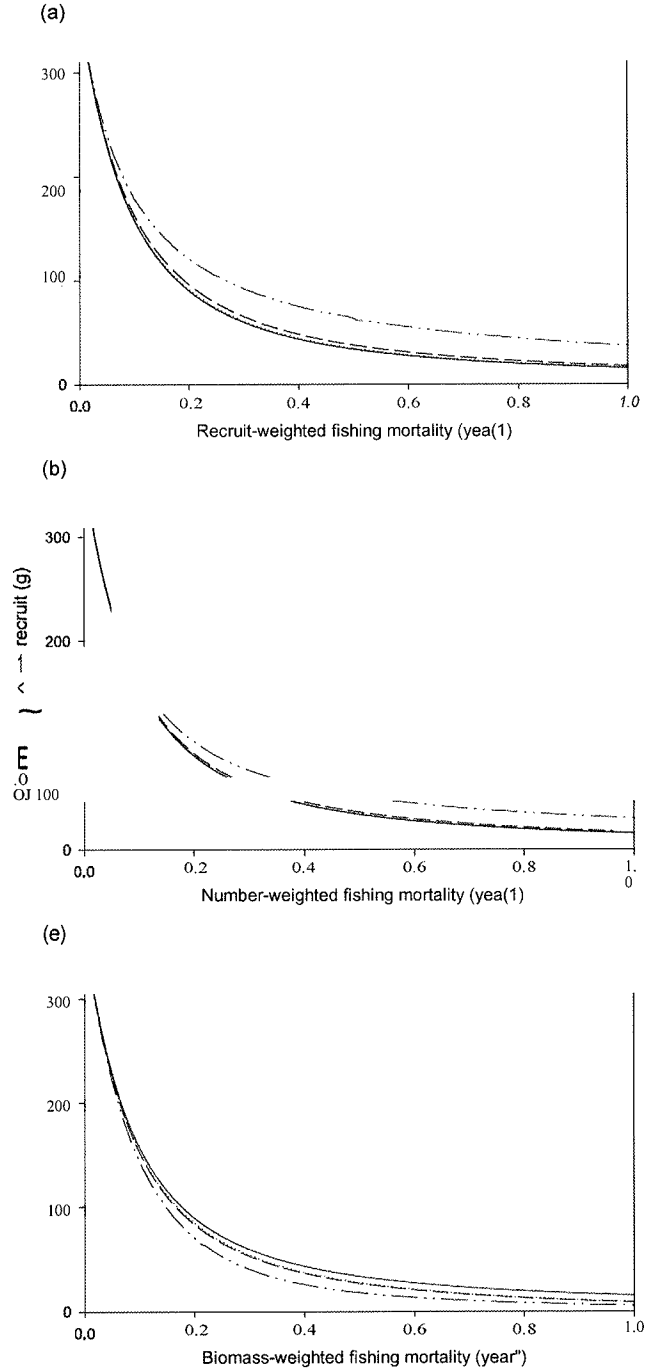
Fig. 3. Individual-based yield-per-recruit (yPR) curves assuming fishing mortality varied uniformly in the interval  $((1 - a)F_0, (1 + a)F_0)$ , where  $a \sim 0$  (solid line), 0.25 (dotted line), 0.5 (broken line), and 1 (broken dotted line). In part (a), the x axis represents recruit-weighted fishing mortality  $F_0$ , whereas in (b) and (c), the x axis is number-weighted and biomass-weighted fishing mortalities, respectively.



nonlinearity of the conventional BPR curve is the greatest. A similar, though quantitatively weaker, pattern is seen when fishing mortality is number weighted. For biomass-weighted mortality, individual variation causes a decreased BPR at a given fishing mortality.

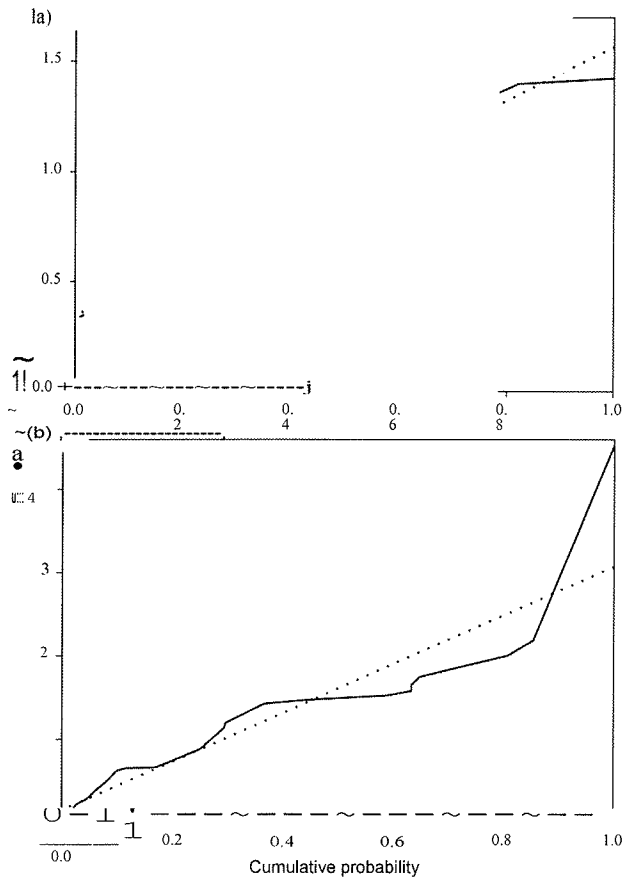
Cumulative probability distributions were estimated for the US. portion of Georges Bank and for the Mid-Atlantic Bight over the years 1982-1994 (Fig. 5). Both CDFs show high spatial variability in fishing mortality, with the highest

Fig. 4. Individual-based biomass-per-recruit (BPR) curves assuming fishing mortality varied uniformly in the interval  $((1 - a)F_0, (1 + a)F_0)$ , where  $a \sim 0$  (solid line), 0.25 (dotted line), 0.5 (broken line), and 1 (broken dotted line). In part (a), the x axis represents recruit-weighted fishing mortality  $F_0$ , whereas in (b) and (c), the x axis is number-weighted and biomass-weighted fishing mortalities, respectively.



fishing mortality located in the most productive areas of the two regions (the Great South Channel area of Georges Bank, and the Hudson Canyon area in the Mid-Atlantic Bight). Variability appears to be higher in the Mid-Atlantic Bight than in Georges Bank. In both cases, the estimated CDFs are

Fig. 5. Estimated cumulative distribution functions of sea-scallop fishing mortality during the years 1982-1994 for (a) the U.S. portion of Georges Bank, and (b) the Mid-Atlantic Bight.



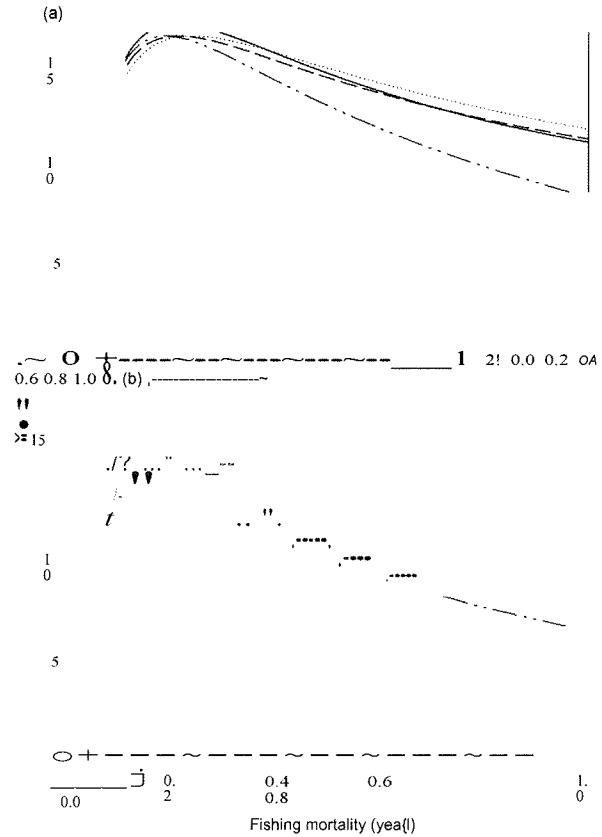
approximately linear; the slight nonlinearities are most likely artifacts of the coarse nature of the survey design. Thus, it is reasonable to approximate both of these empirical CDFs with their best least-squares fitted lines, corresponding to uniform probability distributions.

Individual-based YPR and BPR curves for these two regions are given in Figs. 6 and 7. The higher variability in fishing mortality in the Mid-Atlantic Bight induced a larger deviation from the conventional per-recruit curves in this region than in Georges Bank.

**Discussion**

The analysis performed here indicates that variation in fishing mortality risk among recruits (caused by, for example, spatial variation in fishing mortality) can alter the YPR and BPR that would be predicted by conventional theory. For a typical YPR curve that contains a single inflection point, standard theory will overestimate yield at low fishing mortalities where the YPR curve is concave, and underestimate it at high fishing mortalities where it is convex, when fishing mortalities are recruit-weighted. This is the "Jensen's inequality effect" discussed in the Introduction. Note that the conventional and individual-based YPR curves do not necessarily cross exactly at the point of inflection. Jensen's inequality gives no information in the case where the fishing mortality of some recruits are on each side of the inflection

Fig. 6. Calculated individual-based yield-per-recruit (YPR) for (a) the U.S. portion of Georges Bank, and (b) the Mid-Atlantic Bight. For each curve, YPR plots were created with three different methods of estimating mean fishing mortality on the x axis: recruit-weighted  $F$  (dotted line), number-weighted  $F$  (broken line), and biomass-weighted  $F$  (broken dotted line). The solid line indicates the corresponding standard YPR curve.

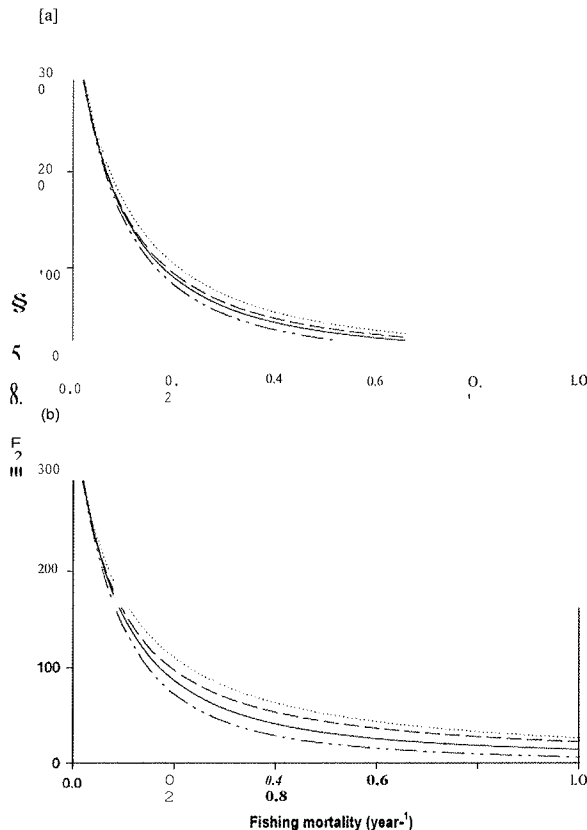


point. Thus, the two lines can cross at any point in a broad range of values near the point of inflection.

More radical departures from the conventional YPR curve are seen when fishing mortality is weighted by number or biomass. As discussed in the introduction, number- and biomass-weighted fishing mortalities tend to overweight the fishing mortality of those recruits whose fishing mortality risk is below average, because these individuals will be overrepresented in the population. The relatively low fishing mortality on this portion of the population masks the high fishing mortality on the other part of the population. This phenomenon is especially apparent when there is high variability in fishing mortality and (or) high mean fishing intensity. The net effect is to lower the number- and biomass-weighted  $F_{m>x}$ , and lower the predicted yield for fishing mortalities above  $F_{max}$  compared with its value when using recruit-weighted fishing mortalities.

Because BPR curves are typically convex, Jensen's inequality implies that individual variation in fishing mortality would increase BPR compared with conventional theory. Intuitively, the increase in BPR from those individuals whose fishing mortality is below the recruit-weighted average is greater than the loss in BPR from those individuals whose fishing mortality is greater than average, thus inducing a net

**Fig. 7. Calculated individual-based biomass-per-recruit (BPR) analysis for (a) the U.S. portion of Georges Bank and (b) the Mid-Atlantic Bight. For each curve, BPR plots were created with three different methods of estimating mean fishing mortality on the x axis: recruit-weighted  $F$  (dotted line), number-weighted  $F$  (broken line), and biomass-weighted  $F$  (broken dotted line). The solid line indicates the corresponding standard BPR curve.**



increase in BPR. This pattern is reversed when biomass-weighted fishing mortality is employed, because the mean biomass-weighted fishing mortality is considerably smaller than the corresponding recruit-weighted fishing mortality, thereby inducing a lower BPR at a given fishing mortality.

Analysis of the U.S. Georges Bank and Mid-Atlantic Bight sea scallop data demonstrates that there was indeed high spatial variability in fishing mortality in these stocks. At the fishing mortalities typical of the 1982-1994 period ( $F \sim 1$ , n-weighted), the results indicate that standard theory would have mildly underestimated both BPR and YPR using **number-weighted fishing mortalities**. However, the use of biomass-weighted fishing mortalities would have induced **the conventional theory to considerably overestimate YPR and BPR**. This suggests that, when applying per-recruit theory, it is not advisable to employ biomass-weighted fishing mortalities. At more optimal levels of fishing mortality, **these YPR curves indicate that spatial variation in fishing mortalities may induce a greater than 10% loss in YPR**.

Motivated by simplicity and the form of the estimated sea scallop CDFs, the analyses conducted here assumed linear fishing mortality CDFs. However, in some cases, the variations in fishing mortality may be more extreme than that im-

plied by uniform distributions, leading to a nonlinear CDF. In such a case, actual YPR and BPR may deviate from those predicted by conventional theory even more strongly than was found here.

The formula of Ssentongo and Larkin has been criticized on the grounds that it is very sensitive to observed lengths near  $L_{\infty}$  (Powell 1979; Hoenig et al. 1983). This was not an issue in the present study because high mortality rates kept most of the population lengths well below  $L_{\infty}$ . In cases where there are substantial numbers of individuals near  $L_{\infty}$ , alternative estimators of mortality, such as those derived by Beverton and Holt (1956) or Powell (1979), should be used. To check the robustness of Ssentongo and Larkin formula in the present case, I compared these estimates of mortality to that obtained by the Beverton and Holt estimator. Timeaveraged mortality for survey strata obtained from the Beverton and Holt formula deviated on average from that of Ssentongo and Larkin by less than 8%, and the overall mean fishing mortalities for the two methods were within 2% of each other. Thus, the mortality estimates in the present study do not appear to be strongly sensitive to the form of the mortality estimator that is employed. Further discussion of relative merits of various methods of estimating mortality rates from length-frequency data can be found in Wetherall et al. (1987).

A strong correlation was observed between productivity (as measured by mean recruitment) and fishing mortality, indicating that fishers were generally concentrating on those areas where catch rates were the highest. Differences in fishing costs among regions can also lead to spatial variations in fishing mortality, with higher fishing mortalities in the lower-cost areas. Such behaviour can be more economically efficient than spatially uniform fishing. A "utility-per-recruit" analysis that calculates, e.g., net revenue per recruit, may be of more interest to managers and fishers in this case than YPR analysis (Die et al. 1988). If costs and prices are known as a function of space and size, it would be straightforward to extend the theory presented here to compute individual-based utility per recruit.

While the emphasis here is on broad spatial variation in fishing mortality, the theory developed can be applied to any situation where fishing mortality risk varies among recruits. For example, recruits that were born at different times of the year might experience different fishing mortality risks. Local refugia could lower the fishing mortality risk for some recruits, again inducing individual variation in that quantity. Even in more mobile species, phenomena such as spawning aggregations may induce variations in fishing mortality risk within the stock.

Similar techniques could also be applied to analyze the effects of individual variations in growth and (or) natural mortality. However, the effects of variability of these factors on YPR are likely to be smaller than those stemming from individual differences in fishing mortality, because the nonlinearity in the relationship between YPR and BPR and fishing mortality is much stronger than that of growth or natural mortality.

If the fishery management system lacks any spatial controls on fishing of sedentary stocks, my results indicate that at fishing mortalities near  $F_{max}$  a reduction in yield compared to spatially uniform fishing will likely occur owing to

the concomitant variations in fishing mortality among recruits. Further losses may occur if a number-or biomass-weighted fishing mortality metric is improperly matched with a standard YPR  $F_{\max}$  target, thereby causing the stock to be subtly overfished,

Some type of area management is therefore necessary in sedentary stocks to maximize yield. One possibility is to manage high- and low-productivity regions separately, as is currently being done in the Canadian sea-scallop fisheries. A second possibility is an area rotation system. Temporarily closing areas with high densities of small animals can help reduce the loss of yield that would occur from localized overfishing of these areas. Rotational systems have been successfully implemented for a number of sedentary invertebrate stocks, and are currently under consideration for the U'S, Atlantic sea scallop fishery.

Even if area management is not practical, managers should at least employ a recruit-weighted fishing mortality metric that matches more closely the standard YPR theory. Alternatively, if it is desired to retain number-or biomass-weighted fishing mortality metrics, reference points need to be set to the corresponding individual-based number-or biomass-weighted maximal YPR, rather than the standard YPR reference points.

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