The Effect of Maternal Age of Spawning on Estimation of F_{msy} for Alaska Pacific Ocean Perch

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Abstract

Recent laboratory research suggests that rockfish larval survival rates increase with the age of the spawner, thus potentially necessitating more conservative harvest policies that explicitly consider the age structure of the spawning stock biomass. In this study, we use simple deterministic population dynamic equations to examine the effect of reduced survival of larvae from younger females on commonly used fishing rate reference points such as F_{msy} and $F_{xx\%}$, the fishing rates corresponding to the maximum sustained yield and conservation of *xx%* of the reproductive potential per recruit relative to an unfished population, respectively. Reduced survival of larvae from younger females results in reduced reproductive potential per recruit for a given level of fishing mortality and also increased estimated resiliency, which results from the estimated recruitments being associated with a reduced measure of reproductive potential. For Bering Sea/Aleutian Islands and Gulf of Alaska Pacific ocean perch, these two effects nearly counteract each other, producing F_{msy} estimates that were relatively insensitive but decreased slightly as maternal effects were considered. Estimates of $F_{xx\%}$ rates that correspond to F_{msy} proxies are more conservative (i.e., cor-

respond to reduced fishing intensity) when uncertainty in the degree to which maternal age affects reproductive potential is considered, as compared to analyses using spawning stock biomass as reproductive potential. These results indicate that estimated stock resiliency is not necessarily independent of the life-history parameters describing production of reproductive potential.

Introduction

Declines in rockfish populations off the U.S. West Coast (California, Oregon, and Washington) have occurred during the past two decades, resulting in the development of rebuilding plans for several species and the declaration of the U.S. West Coast fishery as a "failure" by the U.S. Secretary of Commerce (Parker et al. 2000, Dorn 2002). The collapse of several West Coast rockfish populations has drawn increased attention to rockfish fishery management policies, which, historically, were based on the principle of conserving 40% of the estimated spawning stock biomass per recruit (SPR) obtained from an unfished population. The fishing mortality reference point of $F_{40\%}$ which conserves this level of SPR originated from Clark (1993), who used stochastic simulations to show that $F_{40\%}$ produces a large fraction of the equilibrium maximum sustainable yield (MSY) and reduces the likelihood of low biomass for stocks described with a plausible range of stock-recruitment curves and levels of recruitment autocorrelation. Based on these results, Alaska groundfish are managed by using $F_{35\%}$ as limiting harvest rate and proxy to F_{msy} (the harvest rate associated with MSY) in cases where MSY cannot be reasonably estimated, and $F_{40\%}$ is used as a target harvest rate. Criticisms of the $F_{40\%}$ policy have primarily focused on two issues: (1) stock-recruitment curves typical for rockfish may be less productive than the range considered by Clark (1993), suggesting that policies that conserve more than 40% of the unfished SPR may be appropriate; and (2) harvest policies for rockfish must recognize the reduction of reproductive potential (defined as the output of the spawning process (e.g., eggs or larvae) which provides the basis for stock replacement) associated with the truncated age compositions of exploited populations (Leaman 1991, Berkeley et al. 2004b).

For West Coast rockfish, analyses of stock-recruitment data suggest that fishing mortality rates more conservative than $F_{40\%}$ are appropriate. Dorn (2002) conducted a Bayesian meta-analysis of rockfish stock-recruitment data and found West Coast rockfish stocks to be generally less productive than stocks considered by Clark (1993), and suggested that a risk-neutral harvest rate policy of $F_{50\%}$ is appropriate for these stocks. Additionally, Clark (2002) recommended that for stocks with low resiliency, SPR rates of $F_{50\%}$ or $F_{60\%}$ may be required to maintain an adequate balance of maximizing yield while preserving stock size.

Research on the reproductive biology of rockfish suggests that the reproductive potential of the stock may be a function of the age structure, in particular the proportion of old fish in the population. Leaman (1987, 1991) noted that rockfish are long-lived with little somatic growth in older fish, allowing older fish to allocate a large proportion of available energy to reproduction. The removal of older females by fishing thus disproportionately reduces spawning output such that reproductive value (the lifetime expected number of offspring from a female of a particular age in a stable age distribution) is highly sensitive to increases in fishing mortality. Additionally, Berkeley et al. (2004a) found in laboratory studies that older black rockfish (*Sebastes melanops*) produced larvae with increased survival rates; thus, exploitation can be expected to disproportionately remove the most effective spawners. The implication from these studies is that simply conserving spawning biomass is not sufficient, and managers should aim to preserve spawning biomass with a desirable age structure.

Given the collapse of several West Coast rockfish species, considerable interest exists in determining whether management policies for Alaska rockfish are sufficiently conservative. A panel charged with evaluating the $F_{40\%}$ policy for Alaska groundfish (Goodman et al. 2002) suggested that the currently used $F_{40\%}$ policy may not provide sufficient conservation for Alaska rockfish. Dorn's (2002) meta-analysis is the only study that simultaneously considered the productivity of both West Coast and Alaska rockfish, evaluating eight West Coast stocks, one British Columbia Pacific ocean perch (POP) stock, and three Alaska POP stocks (at that time, Bering Sea and Aleutian Islands POP were assessed as separate stocks). The Alaska POP stocks show greater resiliency (increased slope of the stock-recruitment curve at the origin) than the West Coast stocks, with MSY occurring at SPR rates of approximately $F_{30\%}$. The finding of observed greater resiliency in the Bering Sea/Aleutian Islands (BSAI) POP and Gulf of Alaska (GOA) POP has been repeated in recent stock-recruitment analyses, which have found that estimated F_{msy} reference points are greater than the proxies of $F_{40\%}$ (i.e., $F_{msy} > F_{40\%}$; Spencer and Dorn 2003, Hanselman et al. 2004). However, these studies did not consider how changes in age structure may affect estimates of stock productivity and estimation of harvest reference points such as F_{msy}. For example, the analyses of Clark (1991,1993) evaluate the correspondence of F_{msy} and $F_{xx\%}$ (the fishing rate corresponding to conservation of *xx%* of the reproductive potential per recruit relative to an unfished population) when spawning stock biomass (SSB) is used as a measure of stock reproductive potential. How would expressing reproductive potential in units that reflect differential spawning effectiveness between age groups change the results of Clark's (1991,1993) analyses, and what would be the effect on the estimate of F_{msy} for a particular stock?

The purpose of this study is to consider the effect of the maternal age of spawning on F_{msy} and proxies to F_{msy}. The analysis consists of converting measurements of reproductive potential from spawning stock biomass to "viable larvae," the per-unit production of which is a function of spawner age. First, we consider under what conditions this redefinition may be expected to affect estimates of fishing reference points. Second, we use deterministic population dynamics equations to illustrate the effect on estimation of F_{msy}, assuming that stock-recruitment parameters are well estimated. Third, we estimate F_{msy} for BSAI and GOA POP using a variety of measures of reproductive potential, and compare these estimates to currently used fishing mortality reference points. Finally, we illustrate how common fishing rate proxies to F_{msy} that aim to conserve a specified proportion of the reproductive potential per recruit are affected by maternal effects on larval viability.

Methods

Standard population dynamics equations were used to estimate yield-per-recruit and spawning biomass-per-recruit as a function of fishing mortality for a population with life history characteristics equivalent to those estimated for BSAI POP. These life history parameters describe a stock with relatively low natural mortality ($M = 0.05$), moderate von Bertalanffy K parameter ($K = 0.17$), and age at 50% selection in the fishery less than age at 50% maturity (Fig. 1a), and are viewed as broadly representing common life-history characteristics of exploited rockfish in the North Pacific. Little information is available regarding fecundity of Alaska POP, although studies in other areas indicate that larger females attain fecundities of 305,000 (Hart 1973) and 350,000 (Leaman 1991). A fecundity-at-age relationship for Alaska POP was obtained from fitting an asymptotic curve to Vancouver Island POP data (Dr. Bruce Leaman, International Pacific Halibut Commission, pers. comm.).

Viable larvae are introduced as a measure of reproductive potential that discounts the output from younger spawners via a larval survival curve. Viable larvae were estimated as

$$\text{Viable larvae} = \sum_a s_a f_a m_a p_a N \qquad (1)$$

where N is total number of female fish, p_a is the proportion at age, m_a is the proportion mature at age, f_a is fecundity at age, and s_a is proportion of larvae surviving to two weeks.

Two separate larval survival curves were considered: (1) a proxy curve adapted from the black rockfish laboratory data of Berkeley et al. (2004a); and (2) a knife-edged curve in which no larvae produced from a female younger than 20 years would survive. Berkeley et al. (2004a) develop an asymptotically increasing relationship between maternal age and the time required for 50% mortality of black rockfish larvae, and

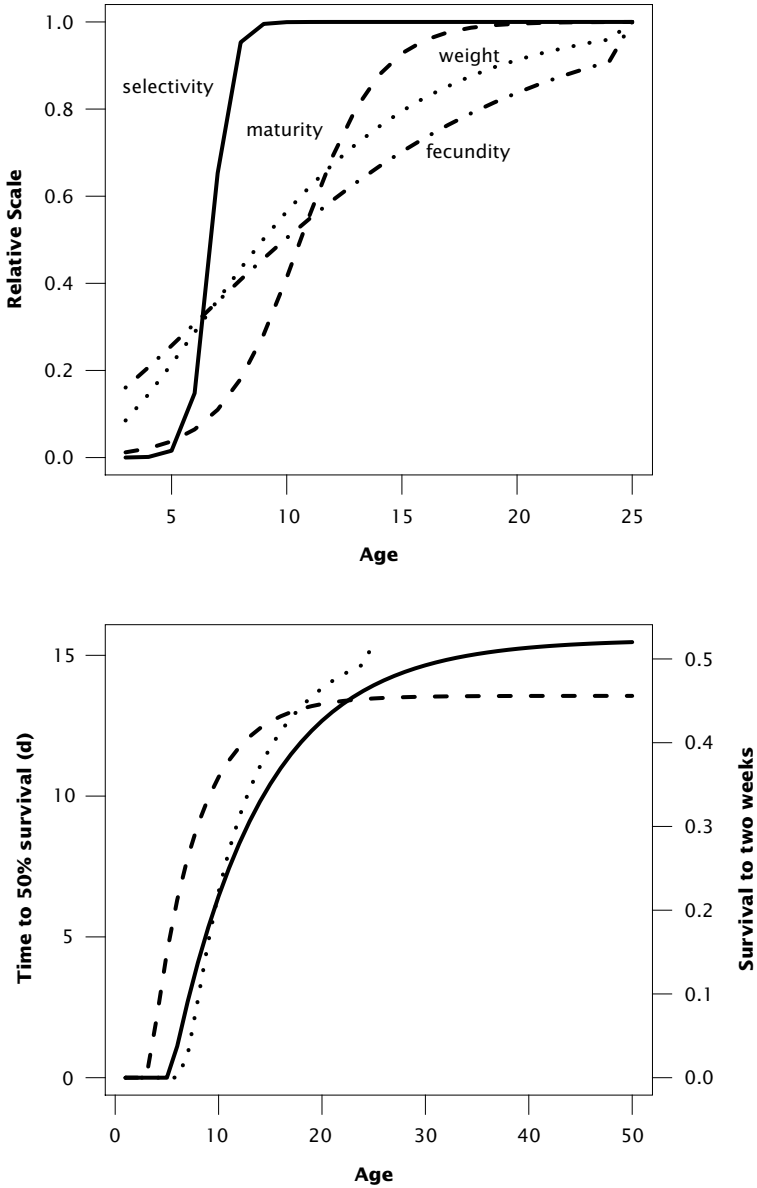

Figure 1. (a) Selectivity, maturity, weight, and fecundity at age used to model BSAI POP, all shown on a relative scale. (b) Days to 50% survival for black rockfish larvae (dashed line; from Berkeley et al. 2004a) as a function of spawner age, and modified curve used for POP (solid line); the estimated proportion of POP surviving to two weeks (shown for ages 3-25+) is shown in the dotted line.

this relationship was modified to model larval mortality rate for POP (Fig. 1b). Relative to black rockfish, POP have both a longer generation time and older age at maturity. The curve describing time to 50% larval mortality for POP thus had a higher x-intercept and lower slope to reflect these considerations and was used to calculate the proportion of larvae surviving two weeks, a period arbitrarily chosen to provide some contrast in the larval survival rates by age. The knife-edged survival curve provides a scenario of extreme maternal effects on reproductive potential, thus creating contrast between measures of reproductive potential that consider intermediate and no effects on larval survival, represented by the larvae produced with the proxy curve and SSB, respectively.

A Beverton-Holt recruitment curve was used for computation of equilibrium yield and was re-parameterized using R_0, the expected recruitment consistent with the reproductive potential of an unfished stock S_0, and a parameter that measures the resiliency of the stock, h, defined as the proportion of R_0 that recruits when the reproductive potential of the stock is reduced to 20% of S_0 (i.e., the steepness parameter of Mace and Doonan 1988). The reparameterized Beverton-Holt curve is given by

$$R = \frac{0.8\, R_0\, h\, S}{0.2\varphi_0\, R_0(1-h) + (h-0.2)S}, \qquad (2)$$

where S is reproductive potential (either SSB or viable larvae), φ is either SSB or viable larvae-per-recruit (defined as SPR and LPR, respectively), and $S_0 = \varphi_0 R_0$ for an unfished stock. Steepness ranges between 0.2 (recruits related linearly to reproductive potential) to 1.0 (recruits independent of reproductive potential). Equilibrium recruitment and yield were obtained for a sequence of harvest rates where LPR and SPR is reduced to a fraction p of unfished LPR or SPR (p = 1.00,0.99, . . .,0.01), and F_{MSY} was estimated as the instantaneous fishing mortality rate associated with the level of p at which equilibrium yield is maximized.

Application to Alaska POP

Estimates of F_{msy} for GOA and BSAI POP using larvae (produced with either the proxy or knife-edged survival curve) and SSB as measures of reproductive potential were made with a Bayesian estimation procedure. Time series of numbers at age, including recruits, for each stock were obtained from age-structured stock assessments (Spencer et al. 2004, Hanselman et al. 2003), and estimates of viable larvae were made from Eq. 1 using the appropriate life-history parameters from each region. There are three parameters for which priors need to be developed, h, R_0, and σ^2, the variance of expected recruitment. The prior for steepness was modeled by assuming that β, the logit of h, was normally distributed (after rescaling h into the interval (0,1), $(h-0.2)/0.8$, and simplifying),

$$\beta = \log\left(\frac{h-0.2}{1-h}\right),\ \beta \sim \mathrm{N}(\mu,\xi^2). \qquad (3)$$

For h in the interval (0.2,1.0) the logit β ranges from $-\infty$ to $+\infty$, allowing straightforward specification of a mean and variance. A normal prior was used for R_0, and a locally uniform prior for σ on a log scale was used. The log joint posterior distribution is the sum of the log-likelihood and the log prior, and the mode of the joint posterior distribution was obtained using the AD Model Builder nonlinear optimization software (Otter Research 1996).

The prior for β was based on levels of reproductive success (defined as R/S at the origin divided by R_0/S_0) considered plausible for rockfish. Dorn et al. (2003) generated a prior distribution by using a level of reproductive success of 8 ($\beta = 0.34$) as the midpoint of the distribution (corresponding to the middle of the range of stock-recruitment curves considered by Clark 1991), and set the prior variance so that reproductive success values of 4 and 16 were located at the 10th and 90th percentiles of the distribution. For Alaska POP, the same variance was used but the midpoint of the distribution was lowered to reflect a level of reproductive success of 4 ($\beta = -0.51$), thus reflecting the perceived lower productivity of rockfish relative to the values considered by Clark (1991). The midpoint of this distribution corresponds to a steepness of 0.50, closer to the value of 0.39 found for five rockfish stocks in a meta-analysis by Myers et al. (1999). Prior estimates of R_0 were derived from estimates of recruits consistent with the stock size in the first year of the age-structured stock assessment model, and a relatively large coefficient of variation of 0.22 was assigned.

Estimation of fishing rate proxies to F_{msy}

The relationship between equilibrium yield and fishing mortality requires knowledge of the stock-recruitment parameters h and R_0, and for cases where these parameters are unknown Clark (1991, 1993) proposed examining yield curves for a range of potential stock-recruitment relationships in which the level of reproductive success ranged from 4 to 16. The "maximin" criteria, defined as the maximum of the minimum equilibrium yield for each level of fishing mortality, was used to identify the optimal fishing rate, expressed as $F_{xx\%}$, to be used as a proxy to F_{msy}. In this study, the same methodology is applied to examine how the index of reproductive potential may affect the harvest rate proxies. Consistent with Clark (1991,1993), yield curves corresponding to the levels of reproductive success of 4 and 16 (corresponding to steepness values of 0.5 and 0.8, respectively) were produced for each of the three measures of reproductive potential (intermediate levels of reproductive success did not affect the maximin fishing mortality rate), and the optimal fishing rate proxy was then identified explicitly considering

uncertainty not only in stock-recruitment relationships, but also the degree to which spawner age affects larval viability.

Results

Spawning stock biomass is commonly used as a proxy for reproductive potential (i.e., eggs produced) in stock-recruitment analyses, and under the assumption of a linear (density-independent) relationship this substitution does not affect the stock-recruitment analyses (Rothschild and Fogarty 1989). Similarly, recasting reproductive potential from SSB to viable larvae will not change the stock-recruitment analysis unless there is a nonlinear relationship between these measures, and this can be evaluated by examining whether the ratio of viable larvae to SSB changes with stock size. Spawning stock biomass can be expressed as the sum over all ages of the product of numbers at age, weight at age, and maturity at age, and the ratio of viable larvae (Eq. 1) to SSB is

$$\frac{Larvae}{SSB} = \frac{\sum_a s_a f_a m_a p_a}{\sum_a w_a m_a p_a} \qquad (4)$$

where w_a is the weight at age. Although density-dependent changes in fecundity, proportion mature at age, and growth may occur for rockfish (Leaman 1991, Gunderson 1997), attention on the production of viable larvae has largely focused on the reduction of the age structure associated with exploited populations (Berkeley et al. 2004b). Thus, the major factor expected to affect the per unit production of viable larvae in the presence of age-dependent maternal effects is p_a, and Eq. 3 provides a framework for assessing how several factors may affect the ratio of viable larvae to SSB.

The relationships between SSB, viable larvae (produced with the proxy curve) and mean age for an equilibrium population with constant recruitment are shown in Fig. 2a. As fishing mortality increases the mean age decreases, resulting in the production of viable larvae decreasing at a greater rate than SSB due to the age-dependant maternal influence on larval survival. Thus, the proportion of viable larvae per recruit conserved, relative to an unfished stock, at any given fishing mortality rate is lower than the proportion of SSB conserved. For example, a fishing rate of 0.049 would conserve 40% of the SSB but only 35% of the viable larvae per recruit (proxy survival curve), and 27% of the viable larvae per recruit (knife-edged survival curve).

Conversely, a reduction in mean age combined with defining reproductive potential as viable larvae rather than SSB results in increased estimated steepness in the stock-recruitment curve. This occurs because although reproductive potential is reduced, the definition of recruits has not been altered. Thus, an identical level of recruits would be associated

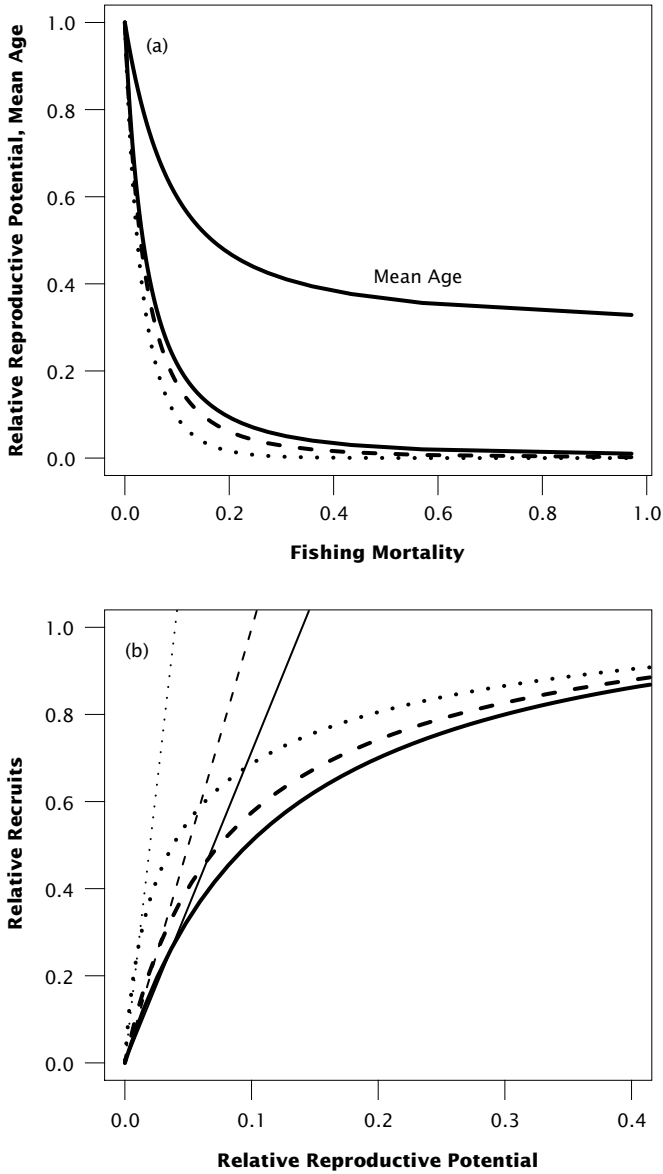

Figure 2. (a) The proportion of SSB per recruit (lower solid line) and larvae per recruit produced with the proxy (dashed line) and knife-edged (dotted line) survival curves, relative to an unfished stock, with increasing fishing mortality; the relative mean age is shown with the upper solid line. (b) Stock-recruitment curves and replacement lines for three measures of reproductive potential, plotted on relative scales: SSB (solid lines), larvae from proxy survival curve (dashed lines), and larvae from knife-edged survival curve (dotted lines). The replacement lines correspond to an *F* of 0.145.

with diminished reproductive potential, resulting in an interpretation of increased steepness h and resiliency. Consider a case where the number of recruits is defined as a function of SSB via the Beverton-Holt curve with a steepness parameter h of 0.7, and increased fishing results in reduced equilibrium SSB and the truncated equilibrium age structure as in Fig. 2a. Relating the number of equilibrium recruits derived from this curve to equilibrium viable larvae (as produced from the proxy curve) results in an estimated steepness of 0.75, whereas relating the same recruits to equilibrium viable larvae (as produced from the knife-edged curve) results in an estimated steepness of 0.85 (Fig. 2b).

The effect of using viable larvae as a measure of reproductive potential on F_{msy} will involve a tradeoff between the greater conservatism implied by the reduced reproductive potential per recruit and the greater resiliency implied by an increased steepness in the stock-recruitment curve. Thus, while the slope of the spawner-recruit curve at the origin becomes steeper with maternal effects, the replacement lines (the recruits per unit of reproductive output) also become steeper for a given level of fishing mortality, and the effect on equilibrium recruitment, yield, and F_{msy} depends on the relative relationship of these two lines. For example, for the stock-recruitment curve with viable larvae (knife-edged curve) the rate of fishing producing equilibrium recruitment of zero (F_{crash}) was 0.145, whereas applying the same F to the stock-recruitment curves for the other two measures of reproductive output produces positive equilibrium recruitment. The estimated F_{msy} also increases from 0.057 to 0.06 when reproductive potential changes from SSB to viable larvae with the knife-edged curve (Fig. 3).

Application to the BSAI and GOA POP data provided contrasting results in which the estimates of F_{msy} decreased slightly as maternal effects are considered. Changes in the definition of reproductive potential noticeably changes the scatterplot of stock-recruitment data; the individual data points are shifted by varying degrees to the left as the recruitment data are associated with diminished measures of reproductive potential (Fig. 4). The stock-recruitment curves derived from these data are shown in Fig. 5, along with the replacement lines corresponding to extinction when reproductive potential is measured as viable larvae with the knife-edged survival curve. The fishing rate associated with this replacement line leads to positive sustained yields when reproductive output is measured as viable larvae (proxy survival curve) or SSB. For the BSAI POP, the estimates of steepness ranged from 0.86 (SSB) to 0.91 (larvae with knife-edged survival curve), whereas the estimates of $F_{40\%}$ decreased from 0.049 (SSB) to 0.033 (larvae with knife-edged survival curve) (Table 1, Fig. 5). Estimated F_{msy} decreased from 0.087 (SSB) to 0.070 (larvae with knife-edged survival curve), and F_{crash} decreased dramatically from 0.35 (SSB) to 0.17 (larvae with knife-edged survival curve) (Table 1, Fig. 6). A similar pattern was seen for

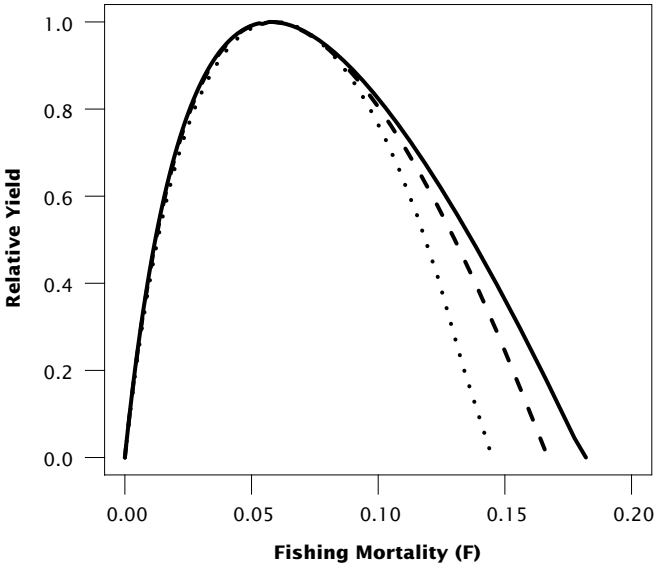

Figure 3. Relative yield as a function of fishing mortality for the stock-recruitment curves presented in Fig. 2b, with reproductive potential defined as SSB (solid line), larvae (proxy survival curve; dashed line), and larvae (knife-edged survival curve; dotted line).

the GOA POP, where steepness increased across the three measures of reproductive potential from 0.81 to 0.93, $F_{40\%}$ decreased from 0.060 to 0.036, F_{msy} decreased slightly from 0.11 to 0.09, and F_{crash} decreased from 0.37 to 0.20.

Incorporation of uncertainty in the degree to which spawner age affects larval survival resulted in estimated proxy fishing mortality reference points being more conservative than those attained from consideration of stock-recruitment uncertainty alone. The yield curves for each of the three measures of reproductive potential are shown in Fig. 7(a-c), and correspond to stock recruitment curves with levels of reproductive success of 4 or 16, spanning the range considered by Clark (1991). With reproductive potential measured in SSB, the proxy fishing mortality rate resulting from the maximin criterion occurs at an F_{spr} rate of $F_{43\%}$, identical to the results of Clark (2002) for Beverton-Holt curves. With reproductive potential defined as larvae (either from the proxy or knife-edged survival curves), the proxy fishing reference points would conserve a similar amount of the reproductive potential, but the fishing mortality reference point would decrease from 0.044 (SSB) to 0.032 (lar-

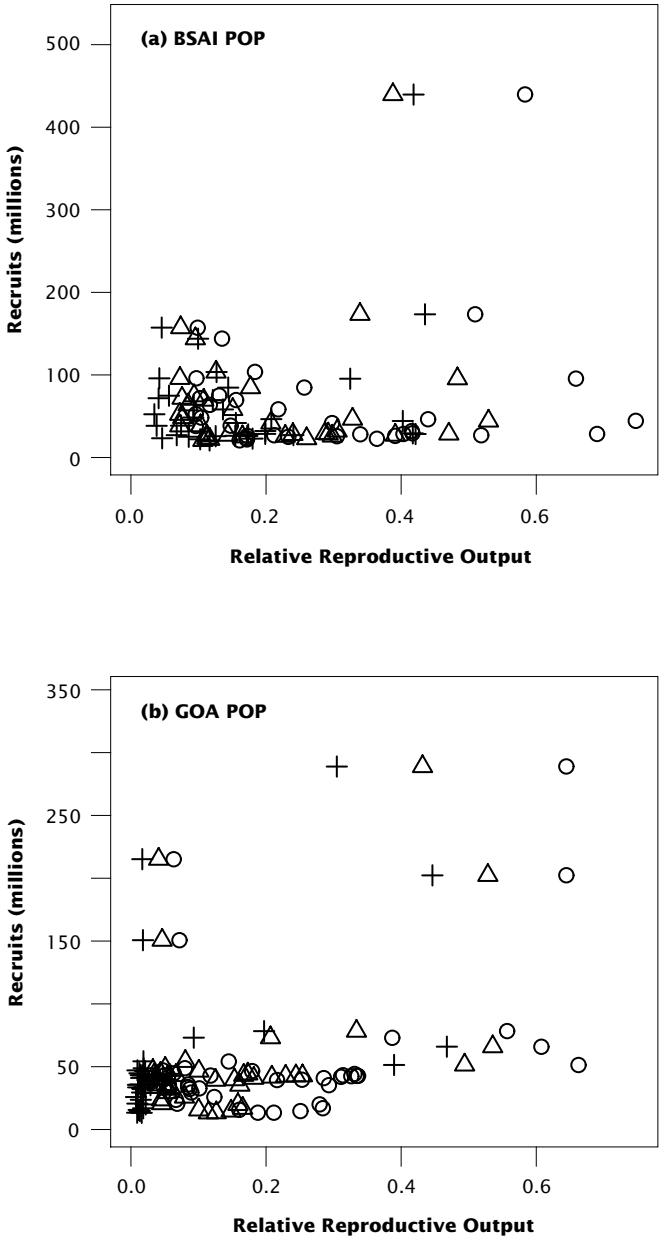

Figure 4. Stock recruitment data for (a) BSAI POP and (b) GOA POP with scaled reproductive potential measured as SSB (circles), larvae from proxy survival curve (triangles), and larvae from knife-edged survival curve (crosses).

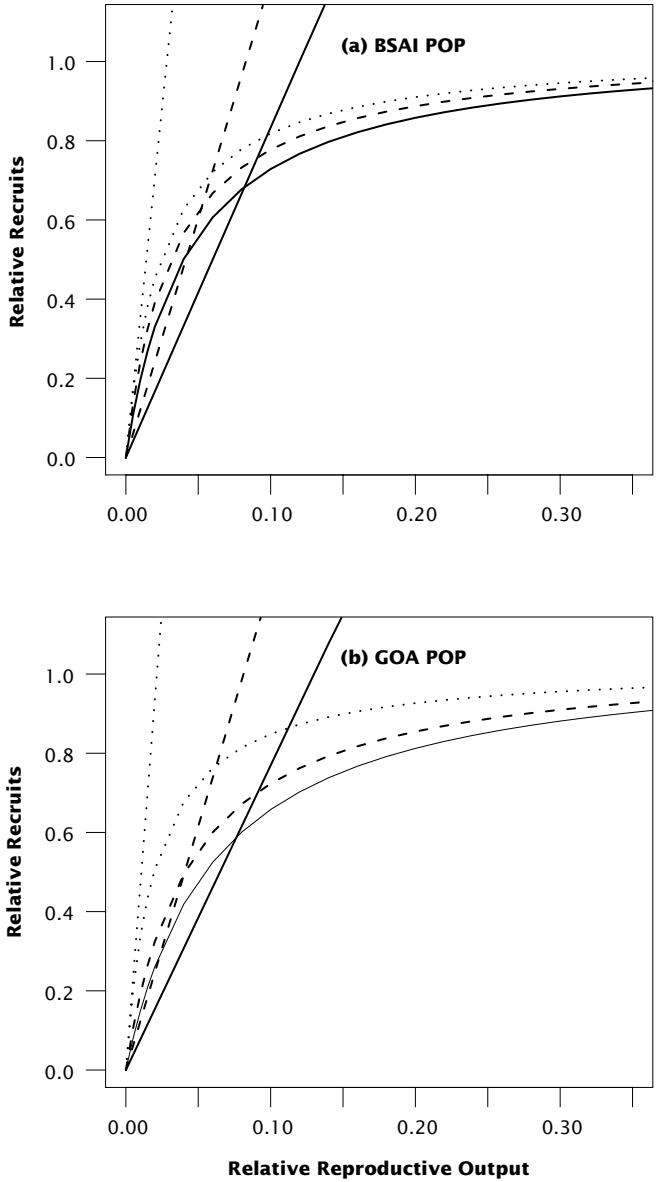

Figure 5. Estimated stock-recruitment curves for (a) BSAI POP and (b) GOA POP with scaled reproductive potential measured as SSB (solid lines), larvae from proxy survival curve (dashed lines), and larvae from knife-edged survival curve (dotted lines). The replacement lines correspond to *F* levels of 0.17 and 0.20 for BSAI and GOA POP, respectively.

Table 1. Estimates of steepness, $F_{40\%}$, F_{msy}, F_{crash}, and proportion unfished SSB or larvae at F_{msy} for BSAI POP and GOA POP with three units of reproductive potential.

Stock	Units of reproductive potential	Steepness	$F_{40\%}$	Proportion unfished SSB or larvae at F_{msy}	F_{msy}	F_{crash}
BSAI POP	SSB	0.86	0.049	0.25	0.087	0.35
	Larvae (proxy mortality)	0.89	0.042	0.21	0.084	0.29
	Larvae (knife-edged mortality)	0.91	0.033	0.17	0.070	0.17
GOA POP	SSB	0.81	0.060	0.24	0.111	0.37
	Larvae (proxy mortality)	0.85	0.049	0.2	0.101	0.29
	Larvae (knife-edged mortality)	0.93	0.036	0.12	0.095	0.20

vae with the knife-edged curve). The yield curves for all three measures of reproductive potential are plotted against F in Fig. 7d, as incorporation of uncertainty in the degree of maternal effects on larval survival in precludes presenting yield curves in terms of relative reproductive potential per recruit. Here, the identified proxy fishing mortality is $F = 0.035$, more conservative than the value of 0.044 that only considers reproductive potential as SSB.

Discussion

Effective reproductive potential of rockfish may be expected to decline at a greater rate than SSB with increased fishing due to a reduced mean age and age-dependent spawner effectiveness (Berkeley et al. 2004a). However, in order to incorporate this observation in operational management advice, it becomes necessary to examine its effect on commonly used reference points such as F_{msy}. It is important to note that although the reproductive potential may be diminished, relative to SSB, the measure of recruits has not been altered. Ideally, one would obtain recruitment estimates from juvenile surveys, although in practice they are typically obtained from stock assessment models utilizing age-composition data from fisheries and surveys. In either case, recruits are simply defined as the number of young fish entering the population. Thus, relating an identical number of recruits with a diminished measure of reproductive potential implies greater estimated resilience, and illustrates that our perception of resilience and stock productivity are not independent of the life-history parameters governing reproductive potential (Morgan and Brattey 2005). The extent to which this estimated increased resilience affects F_{msy} depends on the relative

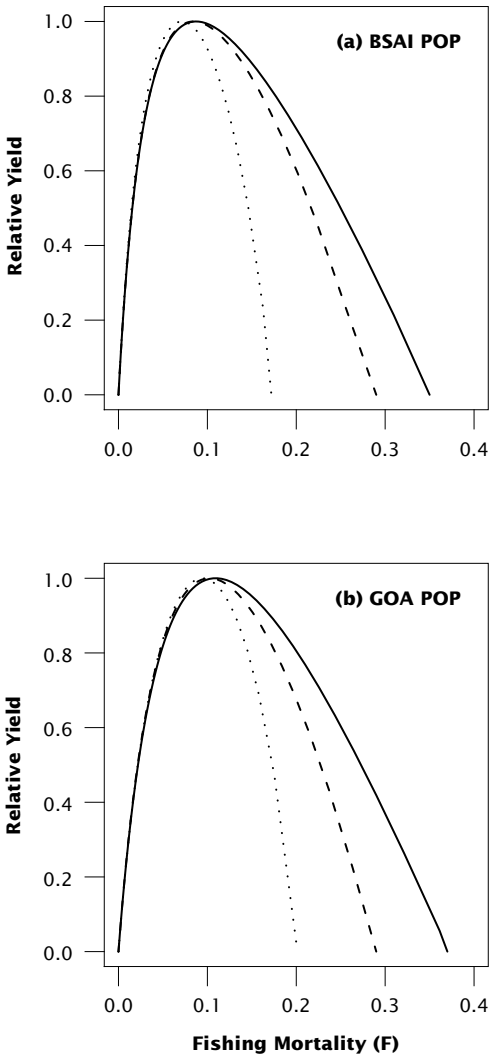

Figure 6. Relative yield as a function of fishing mortality for (a) BSAI POP and (b) GOA POP with reproductive potential defined as SSB (solid line), larvae (proxy survival curve; dashed line), and larvae (knife-edged survival curve; dotted line).

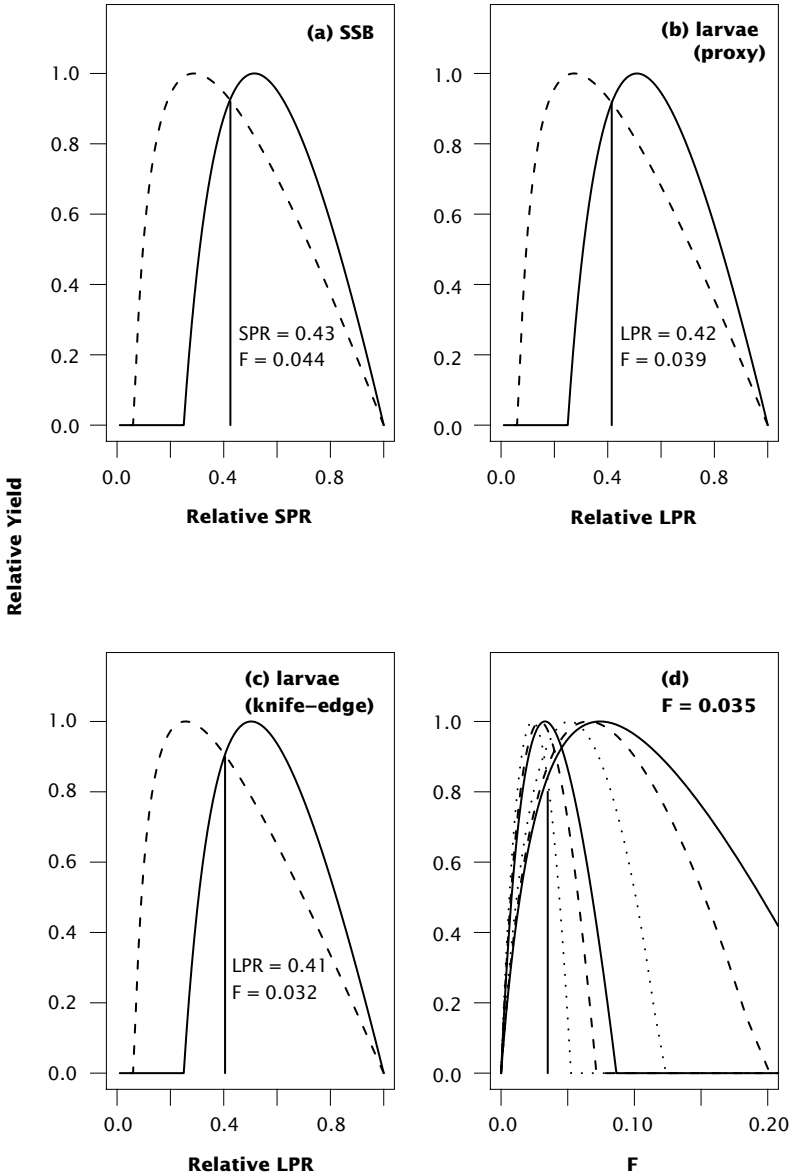

Figure 7. **(a-c) Relative yield as a function of either relative spawner per recruit or larvae per recruit for three measures of reproductive potential with reproductive success of 4 (dashed line) and 16 (solid line); the maximin F_{spr} or F_{lpr} are denoted by the vertical lines. (d) Relative yield for all three measures of reproductive potential and two levels of reproductive success plotted against *F*.**

relationship between the stock-recruitment curve and the replacement lines, which are a direct function of the reproductive output per recruit; thus, age-dependent maternal effects on spawning effectiveness may either increase or decrease F_{msy}. For the theoretical example presented here, the estimated increased resilience was the dominant effect and produced increased F_{msy} with maternal effects. However, for Alaska POP the two opposing processes nearly compensated each other and produced F_{msy} estimates that were relatively insensitive but decreased slightly with maternal effects, whereas F_{crash} decreased sharply. These results are similar to those found for Georges Bank Atlantic cod by Murawski et al. (2001), who found that F_{med} (based on the median level of recruits/spawner) decreased slightly from 0.61 to 0.57 as reproductive potential was converted from SSB to viable larvae, whereas F_{crash} decreased from 1.4 to 0.88.

Consideration of uncertainty in stock-recruitment relationships led to the development of $F_{35\%}$ as a proxy for F_{msy}, and additional uncertainty regarding the extent to which spawner age structure affects reproductive potential would produce more conservative proxy reference points. Similar to the results found by Clark (2002) for Beverton-Holt recruitment curves, the results presented here indicate that conserving approximately 40% of the reproductive potential per recruit is desirable even if the definition of reproductive potential changes from SSB to viable larvae (produced with either the proxy or knife-edged mortality curves). However, the level of fishing mortality associated with these reference points decreases as reproductive potential changes from SSB to viable larvae (produced with the knife-edged curve). For example, if viable larvae (produced from the knife-edged mortality curve) rather than SSB was known to be the appropriate measure of reproductive potential, the F rate used as a proxy for F_{msy} would decrease substantially in this example from 0.044 to 0.032. In practice, there is likely to be uncertainty in the extent to which spawner size/age affects larval viability in addition to the stock-recruitment parameters. Because expressing reproductive potential as SSB represents one bound where these maternal effects are assumed to not occur, any consideration of the maternal effects on reproductive potential were found to produce relatively more conservative harvest rate proxies (Fig. 7).

Given the uncertainty in stock-recruitment relationships for Alaska POP, perhaps the best use of F_{msy} estimates is as a qualitative indicator to assess the need for any directional changes in current harvest rate proxies. The currently used $F_{40\%}$ estimates for BSAI and GOA POP (0.048 and 0.062, respectively) are more conservative than estimates of F_{msy} based on any of the three measures of reproductive potential, suggesting that the current harvest policy is not unduly aggressive given available data on stock productivity. As with much stock-recruitment data, it can be difficult to parse out how much of the recruitment signal

is attributable to spawner output and how much is attributable to environmental conditions. The estimates of high resiliency for Alaska POP derive from a few strong recruitments during favorable environmental conditions in the 1980s, and these results may not be repeated in different environmental conditions. Similarly, much of what we perceive as the low productivity of rockfish recruitment derives from West Coast data collected during a period of unproductive environmental conditions (McGowen et al. 1998), and this interaction between environmental and stock effects, in part, prompted Dorn (2002) to advise cautious interpretation of his meta-analysis results. What is desired is knowledge of how species with rockfish life-history characteristics respond to a variety of environmental regimes, and development of robust management strategies appropriate for this range of environmental variation. For example, low-frequency trends in recruitment can affect the mean age of the stock and thus the indices of reproductive potential and estimation of F_{msy}. Additionally, recruitment variability may be related to longevity (Longhurst 2002), and stochastic simulations can allow examination of the effects of truncated age classes for stocks showing episodic recruitment patterns. Management strategy evaluations (Stokes et al. 1999) appear to be one promising approach for addressing these questions and will be pursued in future research.

Field and laboratory research aimed at documenting the reproductive biology of specific rockfish stocks will greatly assist the interpretation of management importance of maternal effects. Even basic information such as fecundity is absent for many Alaska rockfish stocks, and shows differences between areas for those species where data are available. Although one may never expect to obtain complete knowledge of the influence of spawner age on larval mortality rates in situ, laboratory and field studies that document, for example, the relationship between larval oil globule volume and spawner age can reduce uncertainty for specific stocks and provide a more realistic range of potential maternal effects. A realistic range of the potential influence of maternal effects on larval viability is desired for fisheries management, as this will have a large influence on the harvest rate proxies that will be obtained.

The declines in reproductive potential when maternal age affects larvae viability have also been noted by many other researchers (Scott et al. 1999, Murawski et al. 2001), prompting Berkeley et al. (2004b) to emphasize the importance of older fish in the replenishment of fish stocks and concluding that standard management practices generally do not adequately conserve older fish. However, a complete evaluation of the role of older fish in stock replenishment must not only look at the indices of reproductive potential (i.e., the x-axis of the stock-recruitment plot), but also estimates of stock productivity and management implications resulting from these improved estimates of reproductive potential.

The results of this study are consistent with those of Morgan and Brattey (2005), who found that different measures of reproductive potential can markedly affect perceived stock productivity for Atlantic cod, and demonstrate how information on maternal effects could be addressed within an F_{spr} framework. For future studies, more refined information on rockfish reproductive biology of the type conducted by Berkeley et al. (2004a) would greatly refine our estimates of reproductive potential and the resulting implications for stock productivity.

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