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Incorporation of weight-specific relative fecundity and maternal effects in larval survival into stock assessments

Paul D. Spencer*, Martin W. Dorn

National Oceanic & Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, United States

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ABSTRACT

Marine fish populations may exhibit a number of complexities in their reproductive dynamics, such as weight-specific relative fecundity (i.e. eggs produced per spawner weight increases with spawner size) and maternal effects (i.e. reduced larval survival with reduced spawner age), that are typically not incorporated in stock assessment models. Improved information on reproductive biology could alter estimates of stock productivity and potentially improve estimation of stock–recruitment parameters. In this study, we examined the influence of maternal effects and weight-specific relative fecundity on stock status (defined as reproductive potential and measured as eggs, larvae, or spawning stock biomass), F_{msy}, and the statistical fit of stock–recruitment curves estimated within the Bering Sea/Aleutian Islands Pacific ocean perch (*Sebastes alutus*) and Gulf of Alaska walleye pollock (*Theragra chalcogramma*) statistical catch-at-age assessment models. In each example, estimates of recruitment strength and the variation around stock–recruitment curves were relatively insensitive to various indices of reproductive potential. However, weight-specific relative fecundity increased estimates of F_{msy}, whereas maternal effects decreased estimates of F_{msy}. The range of F_{msy} estimates obtained for walleye pollock from eight indices of reproductive potential was 0.12–0.19, whereas the F_{msy} range for Pacific ocean perch from three indices of reproductive potential was 0.079–0.084. For walleye pollock, weight-specific relative fecundity and recent increases in spawner weight-at-age resulted in an upward trend in reproductive potential relative to constant relative fecundity with spawner size. The two examples demonstrate the influence of reproductive biology upon stock productivity even in cases where residual recruitment variation is relatively unaffected, and motivate the ongoing monitoring of reproductive status and its incorporation in estimation of fishing rate reference points.

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1. Introduction

A fundamental concept in fisheries management is ensuring that harvesting does not compromise stock productivity such that desirable yield and abundance levels cannot be sustained. Stock productivity is typically assessed with stock–recruitment analyses that relate recruitment to reproductive potential, which can be considered the number of offspring (i.e. eggs) which have the potential to become recruits. In practice, spawning stock biomass (SSB) is often assumed to be proportional to total egg production, thus allowing SSB to be used as a proxy for reproductive potential in cases where total egg production is difficult to measure. It has long been observed that potentially misleading stock–recruitment analyses can result when SSB is not proportional to total egg production (Rothshild and Fogarty, 1989), and recent research has revealed a variety of complexities that call into question this proportionality. For example, Rideout et al. (2005) identified several mechanisms for skipped spawning (the failure of mature individuals to spawn), including retention of eggs, resorption of eggs (i.e. mass atresia) and resting of spawners. A recent meta-analysis of fecundity studies for 41 species of rockfish, *Sebastes* spp., off the US west coast found that the eggs produced per spawner weight (i.e., relative fecundity) increased with spawner weight (Dick, 2009), indicating that total egg production is not proportional to SSB. Finally, egg and larval viability may be diminished for young, small, or inexperienced spawners (Trippel, 1998; Berkeley et al., 2004), indicating relatively unequal contribution to reproductive potential. The influence of spawner size/age on egg and larvae viability is an example of a maternal effect, defined generally as the non-genetic contribution of females to the condition of their offspring (Reznick, 1991; Green, 2008), and pertains to the quality of reproductive potential; in contrast; process such skipped spawning and weight-specific relative fecundity pertains to the quantity of reproductive potential produced.

Recognition of these complexities has led to calls to incorporate more realistic measures of reproductive potential into fisheries

* Corresponding author. Tel.: +1 206 546 4248; fax: +1 206 546 6723.
E-mail address: paul.spencer@noaa.gov (P.D. Spencer).

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management (Morgan, 2008; Marshall, 2009). Improved estimates of reproductive potential can potentially affect the estimation of fisheries harvest reference points such as F_{msy} (i.e., the fishing rate that produces the maximum sustained yield) or F_{med} (i.e., the fishing rate associated with a long-term stock replacement) (Murawski et al., 2001; Spencer et al., 2007) and the level of depletion (the reproductive potential of a stock divided by the reproductive potential of an unfished population), two key components of fishery harvest control rules.

Indices of reproductive potential that contain greater biological realism would presumably be expected to improve our knowledge of the stock, provided that the "signal" is not obscured by observation error (or "noise"). Indices of reproductive potential with relatively low information content (i.e. a low signal to noise ratio) may not improve estimates of stock status or productivity relative to more naïve but better estimated indices of reproductive potential. When temporal trends occur in quantities that affect reproductive potential (i.e. maturity at age, sex ratio, and fecundity), which may result from environmental variability and/or changes in population abundance and age structure from fishing, more detailed indices of reproductive potential may result in improved predictions of recruitment; however, this may not necessarily true for cases without temporal trends in reproductive data (Morgan et al., 2011). Additionally, analyses of particular empirical case studies with high levels of observation error may obscure a general understanding of how various reproductive processes, such as maternal effects (i.e. the influence of spawner age/size on the viability of eggs or larvae) and weight-specific relative fecundity, affect estimated stock status and productivity.

A common research approach has been to compare recruitment to several measures of reproductive potential (SSB, female spawning biomass, or total egg production) obtained from assessment model output (numbers-at-age) and data on sex ratio, spawner weight, and fecundity (Marshall et al., 2006; Morgan and Brattey, 2005). In this approach, estimation of depletion and stock productivity from a stock–recruitment analysis are separated from the estimation of stock size, thus assuming that the assessment model recruitment estimates are not influenced by the index of reproductive potential. This approach is reasonable for stocks assessed with virtual population analysis where recruitment models are not considered in the estimation of year-class strength. However, in statistical catch-at-age assessment models where year-class strengths and stock–recruitment parameters are estimated simultaneously with all other model parameters, it is possible that the index chosen for reproductive potential may affect the estimation of recruitment. In these cases, the choice of the index of reproductive potential may affect not only the management choice of defining the inputs to stock–recruitment analyses and estimation of depletion, but also potentially the statistical fit of the assessment model to data.

Maternal effects are an aspect of marine fish reproductive biology that has received a relatively high degree of interest (Green, 2008), and has led, in part, to proposals for consideration of size and age structure in fisheries management policies (Francis et al., 2007). Maternal effects have been shown to reduce the expected lifetime production of reproductive output (O'Farrell and Botsford, 2006) and estimated F_{med} (Murawski et al., 2001) and F_{msy} (Spencer et al., 2007). However, little research has examined how weight-specific relative fecundity can affect estimation of stock status or productivity. Additionally, weight-specific relative fecundity and maternal effects are not necessarily mutually exclusive, and little research has been conducted regarding how these two processes might interact to influence estimation of stock status and productivity.

The purpose of this paper is to use the Gulf of Alaska (GOA) walleye pollock (*Theragra chalcogramma*) and Bering Sea/Aleutian Islands (BSAI) Pacific ocean perch (POP; *Sebastes alutus*) as case studies to illustrate how reproductive information can be incorporated into statistical catch-at-age assessment models. The GOA walleye pollock was examined because of the existence of a time series of spawning stock biomass based on an egg-production survey, as well as a time series of fish maturity data that offers several options for characterizing reproductive potential (Dorn et al., 2010). The BSAI POP was examined because of the potential for maternal effects (Berkeley et al., 2004) and weight-specific relative fecundity (Dick, 2009) in Pacific rockfish. Taken together, the two case studies address several of the issues identified above, including the influence of the variability of input data, and the potential interaction of weight-specific relative fecundity and maternal effects, on estimated fishing rate reference points.

2. Methods

The assessment models used in this paper are slightly modified versions of the models used to provide scientific advice on the management of these stocks by the North Pacific Fishery Management Council (NPFMC) (Dorn et al., 2010; Spencer and Ianelli, 2010). The basic model characteristics are the following: populations are age-structured with annual recruitment; competing mortality due to fishing and natural causes occurs throughout the year; natural mortality is assumed constant for all ages and years; fishing mortality is separable into age-specific selectivity and an annual component, the fully selected fishing mortality. These are fairly standard assumptions that are widely employed in statistical catch-at-age models used by fisheries management bodies.

Models are fit to survey and fishery information using maximum likelihood equations. Survey data consist of an index of population abundance and estimates of age composition. Fishery data include annual fishery take, and estimates of fishery catch-at-age, derived from observer sampling. Log-normal likelihoods are used for index data, while multinomial likelihoods are used for composition data. Parameters estimated include annual recruitment, selectivity parameters for the fishery and the survey, annual fishing mortality, and a survey catchability coefficient for each survey used in the assessment.

For each case study, a stock recruitment curve of the form

$$R = \frac{0.8R_0hS}{0.2\phi_0R_0(1-h)+(h-0.2)S}e^{\varepsilon} \quad (1)$$

was estimated within the statistical catch-at-age model, where S is reproductive potential (i.e. eggs, larvae, or SSB), φ_0 is the expected lifetime production of S per recruit for an unfished stock, R_0 is the estimated recruitment for an unfished population, h is steepness (the recruitment as a proportion of R_0 when S is 20% of the unfished S; Dorn, 2002; Mace and Doonan, 1988), and ε is a normally distributed random error with mean of 0 and standard deviation of σ_r (set to 0.95 and 0.75 for walleye pollock and POP, respectively). The error term e^{ε} thus has a lognormal distribution, and deviations from the mean predicted recruitment were used in the recruitment likelihood equation. The reproductive potential of an unfished stock (S_0) is the product $R_0\ \varphi_0$, and depletion at time t is calculated as S_t/S_0. Note that this differs slightly from the currently used definition of depletion for these stocks, which was based on the mean of estimated recruitment for the post-1977 year classes rather than R_0. Estimates of recruitment, depletion, stock recruitment parameters, and F_{msy} were made for each index of reproductive potential. The model fits to data were evaluated with the total negative ln-likelihood of all data components and the root mean square error

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(RMSE) of the residuals between the log of predicted recruitment and the log of estimated recruitment,

$$RMSE = \sqrt{\frac{\sum_n \varepsilon_i^2}{n}} \quad (2)$$

where n is the number of recruitment estimates.

2.1. GOA walleye pollock

The modeled population includes individuals from age 2 to age 10, with age 10 defined as a "plus" group, i.e. comprised of all individuals age 10 and older (Dorn et al., 2010, Appendix B). The model extends from 1961 to 2010 (50 years). A novel aspect of the GOA pollock assessment model is that selectivity parameters follow a random walk process, which allows selectivity to gradually change over time. The specific data used to fit the model are total catch (1964–2010), fishery length composition (1964–1971), fishery age composition (1972–2009), Alaska Fisheries Science Center (AFSC) Shelikof Strait acoustic survey index and age composition (1981–2010; this also provides estimates of weight at age at spawning), AFSC bottom trawl survey index and age composition (1984–2009), egg production index (1981–1992), Alaska Department of Fish and Game trawl survey index and length (or age) composition, (1989–2010), and historical trawl survey indices and length (or age) composition (1961–1982).

Since the egg production index data has more relevance to this work, it is described in more detail here (see also Picquelle and Megrey, 1993). Egg production estimates were discontinued in 1992 because the AFSC Shelikof Strait acoustic survey was considered to provide similar information. Egg production estimates of spawning biomass are derived from two main components: (1) AFSC ichthyoplankton surveys that estimate the total number of eggs produced, and (2) information on reproductive potential (eggs produced per unit female biomass). Raw ichthyoplankton data (counts of eggs at different developmental stages) are processed extensively to account for the seasonal pattern of spawning and post-hatch mortality. In contrast to most surveys, egg production surveys provide a direct estimate of the spawning population, and do not require estimating a selectivity pattern. While this is advantageous from the perspective of simplicity, it does make the estimates of maturity-at-age, which are used to calculate expected spawning biomass, consequential in fitting stock assessment models. If maturity-at-age estimates are in error, or if they change from year to year when they are assumed constant, model performance could be compromised.

Another issue for both the egg production index and the Shelikof Strait acoustic survey is that only a percentage of the GOA pollock stock spawns in Shelikof Strait. In the assessment model, this percentage is assumed to be constant, and is an estimated parameter (i.e. the catchability coefficient for the survey). Other areas in the GOA have been surveyed, but the time series of estimates are too short to be useful in the assessment. Lack of model fit to both of these indices could be a result of an incorrect assumption that catchability is constant; however, allowing this coefficient to vary inter-annually would imply that the index conveys no information about overall abundance.

A weight–fecundity relationship of the form

$$E = aW^b \quad (3)$$

where E is fecundity (1000s of eggs) and W is spawner weight (g) was obtained from Hinckley (1987), who used data collected from 1983 to 1984 in the BSAI to estimate parameters of $a = 174.92$ and $b = 1.0765$. Data on the proportion mature-at-age have been collected annually in the Shelikof Strait acoustic survey since 1983 and do not indicate a temporal trend, and an average proportion mature from 1983 to 2010 by age is used in the current assessment model (Dorn et al., 2010). Logistic regression was used to estimate maturity ogives and age at 50% maturity ($a_{50\%}$) by year and cohort. Four options for characterizing the proportion mature-at-age were considered: (1) the average proportion mature-by-age from 1983 to 2010; (2) the proportion mature-by-age for the year with the highest $a_{50\%}$; (3) the proportion mature-by-age for the year with the lowest $a_{50\%}$; and (4) time-varying maturity with separate ogives by cohort (with maturity for cohorts with limited data set to the values of the nearest cohort with estimable parameters). Each of the four maturity options can be used to estimate SSB or total egg production, yielding eight potential indices of reproductive potential. For quantities which were time-varying (e.g., fishing selectivity, size-at-age, proportion mature), the calculation of lifetime production of reproductive potential (i.e., the "replacement lines" in stock–recruitment analysis) was based on average values from the most recent five years.

Finally, the general effect of weight-specific relative fecundity was examined with a sensitivity analysis in which the walleye pollock assessment model was run with average proportion mature-at-age and a range of the b exponent in Eq. (3) from 0.8 to 2.0, which corresponds roughly to the 90% credibility interval of the estimated posterior distribution for Pacific rockfish obtained by Dick (2009).

2.2. BSAI POP

The BSAI POP assessment model covers the period from 1961 to 2010, and includes POP between ages 3 and the plus group at age 25. Input data include catch (all years), the AFSC Aleutian Islands (AI) trawl survey biomass estimates (1980–2010), a fishery catch-per-unit-effort index (1969–1978), as well as age and length composition data from the fishery and the AFSC AI trawl survey (Spencer and Ianelli, 2010).

Relative to GOA pollock, information on BSAI POP reproductive biology is more limited and requires assuming that data from neighboring areas are applicable to the BSAI area. The proportion mature-at-age was obtained from Lunsford (1999), who examined POP maturity samples collected in the central GOA. A fecundity-at-length relationship of the form

$$E = x_1 L^{x_2} \quad (4)$$

was fit to POP fecundity estimates for specimens collected in 1985 off Vancouver Island (Leaman, pers. commun.). Specimens were collected in November when the oocytes were expected to be at their maximum unfertilized size, and a gravimetric method was used to estimate fecundity. A weight-at-length relationship of the form

$$W = x_3 L^{x_4} \quad (5)$$

was obtained from specimens collected in the Alaska Fisheries Science Center's Aleutian Islands bottom trawl survey from 1980 to 2006; this relationship was also used to obtain weight at age from the estimates of length-at-age from the Aleutian Islands trawl survey. Substituting Eq. (5) into Eq. (4) yields the fecundity–weight relationship shown in Eq. (3), with the parameters a and b defined as:

$$b = \frac{x_2}{x_4} \quad a = \frac{x_1}{x_3^{x_2/x_4}}$$

Rockfish are viviparous and release larvae, and a hypothesized maternal effect on larval survival was obtained from a modification of the relationship shown by Berkeley et al. (2004) for black rockfish. Berkeley et al. (2004) expressed mortality in units of days to 50% survival, from which we calculated a daily mortality rate.

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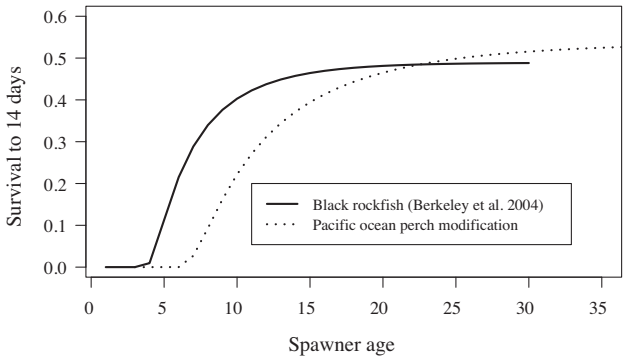

Fig. 1. Survival to viable larvae as a function of spawner age for black rockfish (from Berkeley et al., 2004) and a hypothesized curve for Pacific ocean perch.

Viable larvae were defined as those that survive to 14 days, which was considered a period sufficient for the maternal effect to be expressed. Because POP have lower natural mortality and a longer generation time than black rockfish (Sampson, 2007; Spencer and Ianelli, 2010), the *x*-intercept of the Berkeley et al. (2004) original survival curve was increased and the slope decreased in order to maintain consistency between the ages over which larval viability is hypothesized to be reduced relative to the species life-span (Fig. 1). Three indices of reproductive potential were considered for BSAI POP: (1) SSB; (2) total larvae; and (3) hypothesized viable larvae (which relies on estimated larval production from Eq. (3)). Fishing selectivity varies between four-year blocks in the POP assessment model, and calculation of lifetime production of reproductive potential was based on estimated values from the most recent block.

A Bayesian prior distribution was used to estimate steepness for BSAI POP. Steepness was rescaled into the interval (0,1) and transformed into its logit β, which ranges between $-\infty$ and $+\infty$ and was assumed to be normally distributed (Dorn, 2002; Spencer et al., 2007):

$$\beta = \ln\left(\frac{h-0.2}{1-h}\right), \quad \beta \sim N(\mu, \xi^2) \tag{6}$$

Reproductive success (recruits per spawners at the origin divided by recruits per spawners for an unfished stock) was used to specify the mean and variance of β. The median level of reproductive success for stock–recruitment curves considered plausible by Clark (1991) was 8 (β = 0.34), and this was lowered to 4 (β = −0.51) to reflect a perceived lower productivity of rockfish. The variance of β was set such that the values of reproductive success of approximately 2.3 and 7.7 were located at the 10th and 90th percentiles, respectively. The same Baysian prior for steepness was applied for each of the indices of reproductive potential; thus, any changes in the estimated parameters between the indices of reproductive potential are due to differences in the estimates of recruitment and reproductive potential rather than the prior distribution.

3. Results

3.1. Walleye pollock

The estimated $a_{50\%}$ for walleye pollock year classes between 1984 and 2005 varied between 3.97 and 6.18 without an apparent trend, and show a similar level of variability to values of $a_{50\%}$ fit by year (Fig. 2a). The maximum $a_{50\%}$ of ogives fit by year occurred in 1991 (6.12) whereas the minimum occurred in 1983 (3.51). Estimates of maturity ogives for the pre-1984 and post-2005 year classes were not obtained due to limited data. The weight of spawners has increased over time, particularly since 2003 (Fig. 2b).

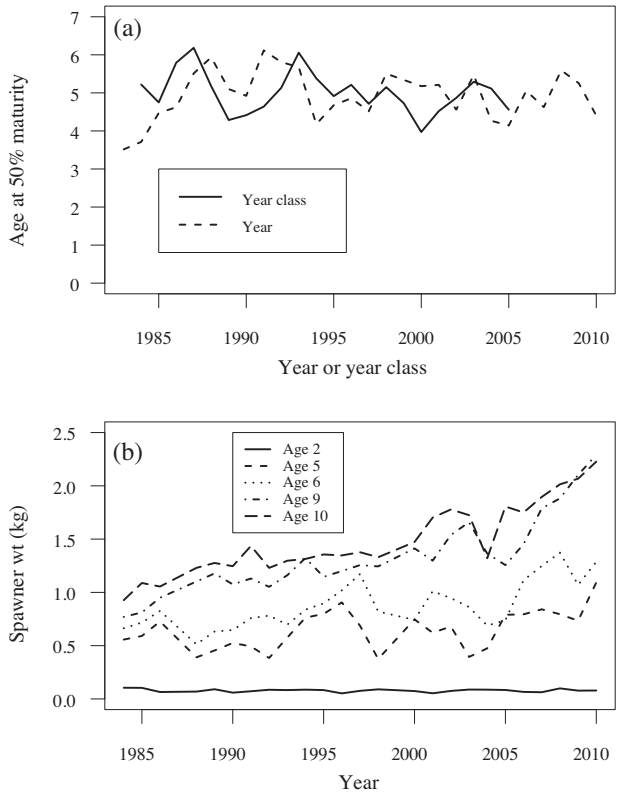

Fig. 2. Walleye pollock age at 50% maturity by year and cohort (a) and temporal trends in spawner weight by age (b).

Estimates of recruitment obtained from stock assessment models with the eight indices of reproductive potential show only slight changes from each other, and appear superimposed on each other in the scale shown in Fig. 3a. The percentage increase from the minimum to maximum recruitment estimates within a year varied from 0.2% to 4.8% across the years, with variation of less than 3% for 43 of the 50 years. The largest percentage change of 4.8% occurred for the relatively low recruitment in 1961 and is not noticeable in the scale shown in Fig. 3a.

Differences in the estimated time series of relative depletion were obtained from the eight different indices of reproductive potential (Fig. 3b). For a given maturity ogive, use of eggs as the index of reproductive potential resulted in slightly lower levels of reproductive output (relative to unfished) than that obtained from using SSB. The maturity ogive with the maximum $a_{50\%}$ resulted in the most variation in relative depletion, as the estimates of relative depletion for these cases were often either the highest or lowest among the eight time series. Estimated relative depletion from the maturity ogives with the minimum and maximum $a_{50\%}$ differed substantially between the mid-1980s and the early 1990s. For example, in 1986 the relative depletion obtained from defining reproductive potential as eggs and using the maturity ogive with the minimum $a_{50\%}$ was 29%, and increased to 46% with the maturity ogive with the maximum $a_{50\%}$.

Estimates of steepness and R_0 varied with the index of reproductive potential, whereas only relatively minor differences were observed in the estimates of RMSE of the recruitment residuals and the overall model fit (Table 1). The highest estimates of steepness were obtained when the maturity ogive with the maximum $a_{50\%}$ was used (0.67 and 0.66 for eggs and SSB, respectively), whereas

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Table 1
Steepness and R_0 estimates and coefficient of variation (CV), and recruitment RMSE and total negative ln-likelihood, as a function of index of reproductive potential for BSAI POP and GOA walleye pollock. The percent change from SSB (for POP) and SSB with the average maturity ogive (for walleye pollock) is shown in parentheses.

Index of reproductive potential	Maturity ogive	R_0 (millions)			Steepness			Recruitment RMSE		Total negative ln-likelihood	
		Est	CV	Pct change	Est	CV	Pct change	Est	Pct change	Est	Pct change
BSAI Pacific ocean perch											
SSB	Based on GOA data	126.07	0.24		0.73	0.10		0.785		427.41	
Total larvae	Based on GOA data	120.50	0.23	(−4.42)	0.75	0.09	(2.59)	0.784	(−0.17)	427.96	(0.13)
Viable larvae	Based on GOA data	123.15	0.23	(−2.31)	0.78	0.07	(5.94)	0.780	(−0.60)	428.56	(0.27)
GOA walleye pollock											
Eggs	Average from 1983 to 2010	1427.42	0.54	(−0.02)	0.59	0.22	(2.08)	1.014	(0.16)	1074.38	(0.01)
Eggs	Based on 1991 data (max $a_{50\%}$)	1160.17	0.41	(−18.74)	0.67	0.22	(16.79)	1.029	(1.63)	1075.25	(0.09)
Eggs	Based on 1983 data (min $a_{50\%}$)	1612.22	0.61	(12.92)	0.54	0.21	(−6.33)	1.004	(−0.79)	1073.77	(−0.05)
Eggs	Time-varying maturity	1424.95	0.39	(−0.19)	0.46	0.44	(−20.02)	1.004	(−0.85)	1075.32	(0.10)
SSB	Average from 1983 to 2010	1427.72	0.53		0.57	0.22		1.012		1074.28	
SSB	Based on 1991 data (max $a_{50\%}$)	1168.88	0.41	(−18.13)	0.66	0.22	(14.41)	1.027	(1.50)	1075.18	(0.08)
SSB	Based on 1983 data (min $a_{50\%}$)	1587.64	0.59	(11.20)	0.53	0.21	(−7.96)	1.003	(−0.88)	1073.71	(−0.05)
SSB	Time-varying maturity	1415.63	0.37	(−0.85)	0.45	0.43	(−21.97)	1.001	(−1.06)	1075.20	(0.09)

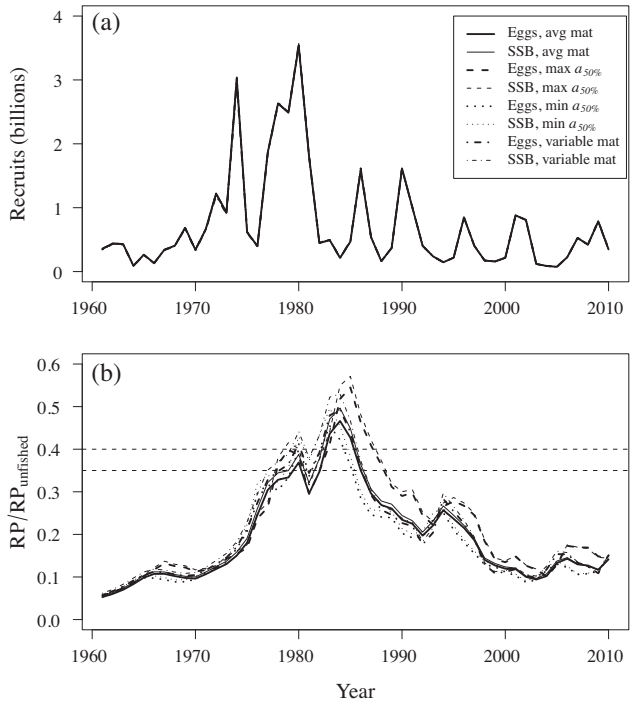

Fig. 3. Estimated walleye pollock recruitment (a) and depletion (b) from assessment models for eight indices of reproductive potential.

the lowest estimates of steepness were obtained with time-varying maturity (0.46 and 0.45). The negative ln-likelihood and RMSE of the recruitment residuals varied slightly among the eight indices of reproductive potential, and showed <0.2% and <3% change, respectively, between the highest and lowest values (Table 1). Higher estimates of steepness corresponded to higher estimates of F_{msy}, which was 0.19 for both eggs and SSB with the maturity ogive with the maximum $a_{50\%}$, and 0.12 for both eggs and SSB with time-varying maturity (Table 2). In contrast, the highest $F_{40\%}$ rates of 0.23 were obtained for the lowest $a_{50\%}$ for each index of reproductive potential, as these values do not reflect changes in estimated stock–recruitment parameters. The coefficient of variation (CV; the standard deviation divided by the mean) of estimated steepness and F_{msy} were approximately 0.43 and 0.71, respectively, with time-varying maturity, whereas the CVs for these quantities for the other reproductive potential indices were approximately 0.21 and 0.34 (Tables 1 and 2). An example stock–recruitment scatterplot is shown in Fig. 4, indicating how estimated stock–recruitment curves can be affected by the units of reproductive potential.

The model fits to SSB values obtained from the egg production index were not improved by inclusion of time-varying maturity (Fig. 5). The negative ln-likelihood to this dataset when eggs were used as reproductive potential with the average maturity ogive was 23.21, and increased to 24.94 with the time-varying maturity ogives.

The sensitivity analysis to the b exponent in the fecundity–weight relationship indicated that the rate of increase of recent egg production (relative to an unfished stock) increased with b (Fig. 6). When $b = 1$, the trend in recent relative egg production was largely flat with some variation. In contrast, increased values of $b > 1$ resulted in progressively stronger increases in relative egg production from 2003 to 2010, which resulted from increased values of b exponentially increasing the influence of the recent trend of increased spawner weights on egg production.

Estimates of steepness and F_{msy} were also sensitive to the b exponent in the fecundity–weight relationship (Fig. 7 and Table 3).

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Table 2
F_{msy} estimates and coefficient of variation (CV), and estimated $F_{40\%}$, as a function of index of reproductive potential for BSAI POP and GOA walleye pollock. The percent change from SSB (for POP) and SSB with the average maturity ogive (for walleye pollock) is shown in parentheses.

Index of reproductive potential	Maturity ogive	F_{msy}			$F_{40\%}$	Pct change
		Est	CV	Pct change		
BSAI Pacific ocean perch						
SSB	Based on GOA data	0.081	0.197		0.062	
Total larvae	Based on GOA data	0.084	0.186	(4.57)	0.062	(−0.693)
Viable larvae	Based on GOA data	0.079	0.167	(−1.68)	0.053	(−14.304)
GOA walleye pollock						
Eggs	Average from 1983 to 2010	0.177	0.336	(2.03)	0.198	(−1.192)
Eggs	Based on 1991 data (max $a_{50\%}$)	0.193	0.343	(11.24)	0.175	(−12.738)
Eggs	Based on 1983 data (min $a_{50\%}$)	0.176	0.335	(1.59)	0.228	(13.754)
Eggs	Time-varying maturity	0.120	0.713	(−30.57)	0.197	(−2.089)
SSB	Average from 1983 to 2010	0.173	0.337		0.201	
SSB	Based on 1991 data (max $a_{50\%}$)	0.188	0.343	(8.41)	0.176	(−12.177)
SSB	Based on 1983 data (min $a_{50\%}$)	0.174	0.337	(0.69)	0.233	(16.181)
SSB	Time-varying maturity	0.117	0.710	(−32.67)	0.199	(−1.084)

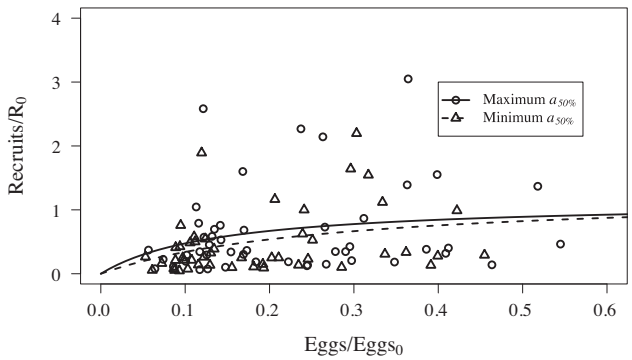

Fig. 4. Scatterplot of estimated recruitment and reproductive potential, and fitted stock–recruitment relationships, for GOA walleye pollock with reproductive potential defined as eggs with maturity ogives with either the maximum or minimum $a_{50\%}$.

Estimates of steepness increased from 0.55 with $b = 0.8$ to 0.77 with $b = 2.0$, a 41% increase, whereas estimates of F_{msy} increased 49% from 0.17 to 0.25 over this range of b. The increases in F_{msy} were associated with decreases in estimated R_0, which decreased 19% over the range of b values. The changes in negative ln-likelihood and RMSE were similar to those observed for the eight indices of reproductive potential, and increased by 0.14% and 2.6%, respectively, over the range of b values.

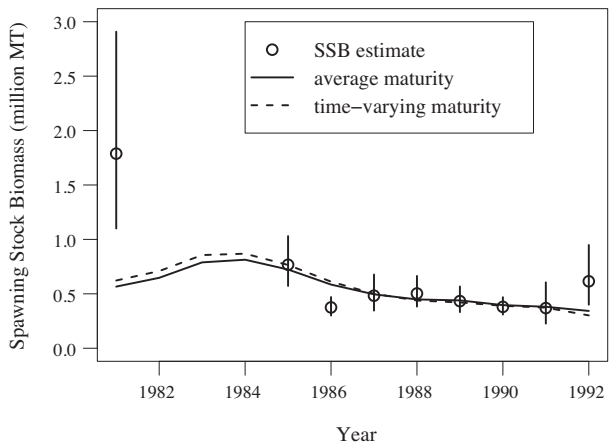

Fig. 5. Model fits to estimates of spawning biomass from the Shelikof Strait egg production survey with reproductive potential defined as eggs with either average or time-varying maturity data.

3.2. POP

An exponential relationship between length (cm) and weight (kg) resulted in estimates of 1.02×10^{-5} and 3.09 for x_1 and x_2, respectively, and an exponential relationship between length (cm) and fecundity estimated from the Vancouver Island POP data resulted in estimates of 1.24 and 3.22 for x_3 and x_4, respectively. These values result in estimates of the a and b of Eq. (1) of 2.01×10^5 and 1.04, respectively, indicating weight-specific relative fecundity for POP.

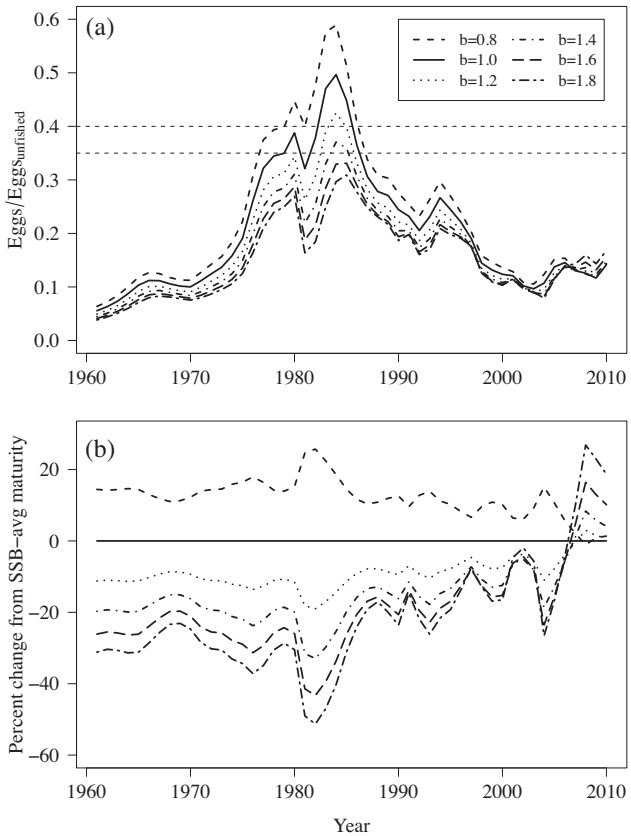

Fig. 6. Estimated depletion (a) for walleye pollock as a function of the b exponent in the fecundity–weight relationship (with the temporal average of the maturity data). The lower panel (b) shows the percentage change in depletion from the case where $b = 1$ (i.e. fecundity is proportional to spawner weight).

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Table 3
Estimated R_0, steepness, F_{msy}, recruitment RMSE, and total negative ln-likelihood as a function of the *b* exponent in the fecundity–weight relationship for GOA walleye pollock. The percent change from $b = 0.8$ is shown in parentheses.

b	R_0 (millions)	Steepness	F_{msy}	Recruitment RMSE	Total negative ln-likelihood
0.8	1410.69	0.55	0.165	1.009	1074.07
0.9	1422.17 (0.81)	0.56 (2.51)	0.169 (2.24)	1.010 (0.17)	1074.17 (0.01)
1	1427.72 (1.21)	0.57 (5.16)	0.173 (4.71)	1.012 (0.35)	1074.28 (0.02)
1.1	1426.58 (1.13)	0.59 (7.96)	0.178 (7.45)	1.014 (0.55)	1074.40 (0.03)
1.2	1418.18 (0.53)	0.61 (10.93)	0.183 (10.48)	1.016 (0.76)	1074.53 (0.04)
1.3	1402.19 (−0.60)	0.62 (14.09)	0.188 (13.86)	1.019 (0.99)	1074.66 (0.05)
1.4	1378.72 (−2.27)	0.64 (17.45)	0.195 (17.62)	1.021 (1.23)	1074.79 (0.07)
1.5	1348.41 (−4.41)	0.66 (21.02)	0.201 (21.80)	1.023 (1.47)	1074.93 (0.08)
1.6	1312.41 (−6.97)	0.68 (24.77)	0.209 (26.42)	1.026 (1.72)	1075.07 (0.09)
1.7	1272.38 (−9.80)	0.70 (28.69)	0.218 (31.50)	1.028 (1.96)	1075.20 (0.11)
1.8	1230.22 (−12.79)	0.72 (32.71)	0.227 (37.01)	1.031 (2.20)	1075.33 (0.12)
1.9	1187.80 (−15.80)	0.75 (36.77)	0.236 (42.91)	1.033 (2.43)	1075.46 (0.13)
2	1146.73 (−18.71)	0.77 (40.80)	0.247 (49.14)	1.035 (2.64)	1075.58 (0.14)

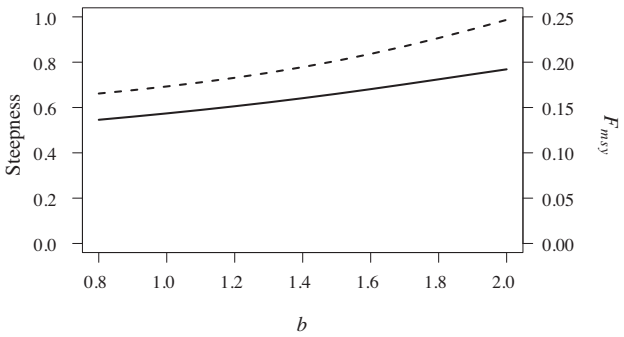

Fig. 7. Estimated F_{msy} (dashed line) and steepness (solid line) (with the temporal average of the maturity data) for walleye pollock as a function of the *b* exponent in the fecundity–weight relationship.

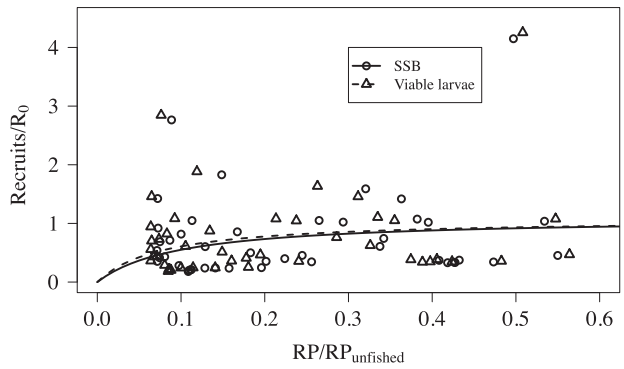

Fig. 9. Scatterplot of estimated recruitment and reproductive potential, and fitted stock–recruitment relationships, for BSAI POP with two indices of reproductive potential.

Similar to the walleye pollock case study, the influence of the reproductive potential index on estimated recruitment was minor, as recruitment estimates for 46 of the 48 year classes differed by less than 2%. Estimates of depletion within a year from the three indices of reproductive potential varied from 4.6% to 35.0% between 1960 and 2010. With the exception of years 1960 to 1963, the lowest and highest estimates of depletion were associated with viable larvae and total larvae, respectively (Fig. 8).

Estimated steepness and F_{msy} differed between model runs with the different indices of reproductive potential, but the relative changes in these quantities were not necessarily in the same direction (Tables 1 and 2). Estimates of steepness and F_{msy} obtained from using total larvae as the index of reproductive potential were 2.6% and 4.6% larger, respectively, than estimates obtained from using SSB as the index of reproductive potential. In contrast, estimates of steepness and F_{msy} obtained from using viable larvae as the index of reproductive potential were 5.9% larger and 1.7% smaller, respectively, than estimates obtained from using SSB as the index of reproductive potential. An example BSAI POP scatterplot (Fig. 9) illustrates a relatively small change in estimated steepness between the cases using either SSB and viable larvae as reproductive potential, as the estimated stock–recruitment parameters for POP are influenced by the prior distribution for steepness. The RMSE values were relatively unchanged between the models with the three indices of reproductive potential. The CVs for steepness ranged between 0.07 and 0.10, whereas the CVs for F_{msy} ranged between 0.17 and 0.20 (Tables 1 and 2).

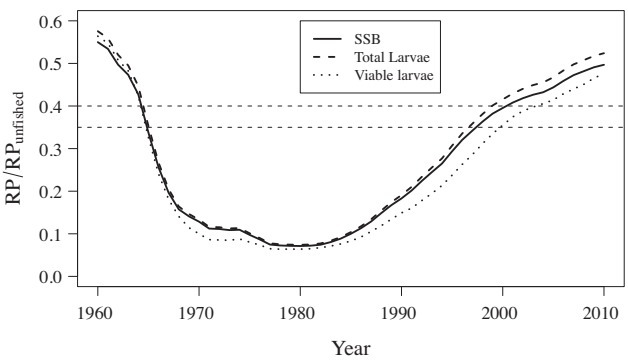

Fig. 8. Estimated POP depletion from assessment models for three indices of reproductive potential.

The indices of reproductive potential were more influential on F_{crash} (the fishing rate where equilibrium recruitment and yield are reduced to zero) than F_{msy}, and estimates of F_{crash} ranged from 0.24 (viable larvae) to 0.28 (SSB) to 0.30 (total larvae) (Fig. 10). This pattern results from stock productivity at high fishing rates and its associated younger age structure being affected to a greater degree by reproductive processes related to spawner age.

4. Discussion

One of the motivations for developing detailed indices of reproductive potential is improving the fit of stock–recruitment curves, but the case studies presented here reveal that more detailed estimates of reproductive biology can substantially affect estimated stock productivity without necessarily improving the statistical fit to stock–recruitment curves. The ability of more detailed indices of reproductive potential and/or indices of age composition to reduce variability around stock–recruitment curves has been observed for cod (*Gadus morhua*) in Iceland (Marteinsdottir and Thorarinsson,

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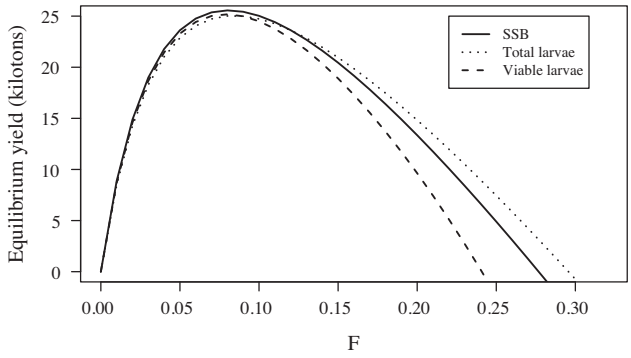

Fig. 10. Estimated POP equilibrium yield with three indices of reproductive potential.

1998) and the Baltic Sea (Köster et al., 2001) but not for cod in the northeast Arctic (Marshall et al., 2006). This range of results is not surprising given that even perfect knowledge of reproductive potential would not address the variability associated with pre-recruit mortality, and observations on pre-recruit abundance are often limited. However, given that estimation of stock productivity and sustainable harvest rates is a primary purpose of stock–recruitment analysis, the influence of information on reproductive biology on estimated stock productivity is, in itself, a sufficient motivation for consideration of these factors.

Among the more critical quantities estimated within age-structured stock assessments are (1) the population abundance; (2) the level of stock depletion; and (3) a recommended rate of fishing that reflects stock productivity. For the two case studies examined here, estimates of depletion and stock productivity were affected by the index of reproductive potential whereas estimates of abundance (i.e. year-class strength) and the variability of deviations from stock–recruitment curves were not substantially affected. This suggests that year-class strength is likely influenced by other factors such as age and length composition data, structural form of selectivity curves, and specification of σ_r. However, our two case studies had substantial age and length composition data, and it is plausible that statistical catch-at-age assessments with a reduced level of age and length composition data may reveal a greater influence of the index of reproductive potential on estimated recruitment.

The results here illustrate that reproductive dynamics such as maternal effects and weight-specific relative fecundity affect stock productivity in a consistent manner. For each of the case studies, the effect of weight-specific relative fecundity (with $b > 1$) was to increase the estimate of F_{msy} relative to use of SSB as reproductive potential (i.e. assuming $b = 1$). This is caused by a higher level of stock productivity being associated with a higher level of reproductive output (relative to an unfished stock) with increased b. Similarly, for POP the incorporation of maternal effects resulted in a reduction of estimated F_{msy} relative to using total larvae as reproductive potential, as maternal effects would be associated with a reduction in reproductive potential and a lower level of stock productivity. For POP, estimation of viable larvae is obtained by first estimating the total larvae, and thus incorporates the combined effects of weight-specific relative fecundity and maternal effects. The opposing effects of these two processes results in the estimate of F_{msy} from viable larvae (0.079) being very similar to that obtained from SSB (0.081), which ignores each process. However, this should not be taken as a reason for not incorporating information on these (and other) complexities of reproductive biology into stock assessments, as the relative degree of influence of these processes would be expected to vary between stocks.

The reproductive biology of marine fish stocks affects not only the stock–recruitment relationship, but also the expected lifetime production of reproductive output. Because estimated productivity (i.e. production of yield or recruitment) is a function of these two aspects, focusing upon only one of these aspects may give an incomplete picture of the influence of reproductive biology on estimated productivity. For example, for the POP case study the lowest level of F_{msy} and the highest level of steepness were obtained from using viable larvae as reproductive potential. In this case, the reduction in the reproductive potential produced per recruit (i.e. the shift in the replacement line) resulted in a low estimate of F_{msy} despite the increased estimate of steepness, and a similar result was obtained in previous applications to Alaska POP (Spencer et al., 2007). Estimation of equilibrium yield integrates the stock–recruitment curve and the expected lifetime production of reproductive output, and thus seems particularly suited for inferring the influence of reproductive biology on estimated productivity.

For the walleye pollock case study, the use of time-varying maturity data did not improve the fit to estimates of SSB obtained from the egg production method, illustrating a case where any underlying trend may be minor relative to the observation error. In theory, time-varying maturity would be expected to improve the fit to the SSB input data, and the lack of improvement reflects the influence of observation errors in at least one of these datasets. Both the maturity information and egg production estimates of SSB are derived from Shelikof Strait and may not be representative of the entire GOA stock. High quality egg and larval surveys can motivate use of indices of reproductive potential as input data for age-structured assessment models. For example, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval index survey (Moser et al., 2001) is used within the US west coast bocaccio (*Sebastes paucispinis*) assessment model (Field et al., 2009) as an index of larval abundance, and fitting this dataset requires information on fish reproduction. However, mismatches in spatial coverage and patchiness of larval spatial distributions have prevented use of CalCOFI larval indices in other stock assessments such as Dover sole (*Microstomus pacificus*) (Brodziak et al., 1997).

As with other inputs to stock assessments models, data on reproductive biology (i.e. maturity, egg production, etc.) will be expected to contain both process and observation errors. In management systems where specification of harvest rates is a function of the estimated uncertainty in fishing rate reference points, such as the US Magnuson-Stevens Fishery Management and Conservation Reauthorization Act, characterizing the uncertainty associated with the reproductive biology is an important step and would not be accomplished by treating the data outside the assessment model as if it were known without observation error. Sensitivity analyses of the type applied here to the GOA walleye pollock are a first-order approach to evaluate the implications of uncertainty. If error bounds to the reproductive data can be specified, the estimation of maturity ogives and fecundity relationships could be conducted within statistical catch-at-age models and would result in estimated variances of fishing rate reference points that reflect the variability of the reproductive data.

Estimated uncertainty in F_{msy} was relatively consistent within each stock with the exception of the use of time-varying maturity ogives for walleye pollock, which evidently introduces variability and results in substantially higher uncertainty in steepness and F_{msy} (CVs of 0.43–0.44 and 0.71, respectively). For the other cases, the lower CVs of F_{msy} for POP (0.17–0.20) than walleye pollock (0.34) likely reflects the use of a prior distribution for steepness in the POP assessment. If the variability in estimated F_{msy} was sufficiently high such that the F_{msy} estimate was considered unreliable for management purposes, one could use $F_{spr\%}$ rates to establish recommended fishing rates. However, $F_{spr\%}$ estimates are also sensitive to information to information on reproductive biology. For

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example, the $F_{40\%}$ values for walleye pollock using eggs ranged from 0.18 to 0.23 for the various options for treating maturity ogives, which is higher than the range of F_{msy} point estimates (excluding the time-varying maturity case) of 0.18–0.19. This illustrates the importance of information on reproductive process regardless of whether fishing rate reference points are based upon F_{msy} or $F_{spr\%}$.

Monitoring of reproductive processes may be especially critical in cases with strong temporal trends that could affect the prediction of recruitment (Morgan et al., 2011) or estimation of current fishing rate reference points. Temporal patterns in recruitment also reflect life-history strategies; for example, POP have been classified as a "periodic" strategist (King and McFarlane, 2003) characterized by high longevity, decadal-scale recruitment patterns, and infrequent strong-year classes. The walleye pollock case study also illustrated that temporal trends in growth rates can interact with reproductive processes such as weight-specific relative fecundity to produce trends in the relative depletion of reproductive potential. Ongoing monitoring will be required to identify such temporal trends and the level of variation in reproductive processes, and would improve stock assessments relative to cases where information on reproductive biology is obtained from data sampled in a single year.

The results of this study illustrate how estimates of depletion and F_{msy} depend on the choice of index for reproductive potential, and demonstrate how processes such as weight-specific fecundity, maternal effects in larval survival, and temporal trends in growth can interact to produce complex changes in estimated stock status and productivity. In future studies, the "signal to noise" properties of reproductive data should be explored more thoroughly, particularly in the context of the other input data to stock assessments. For example, incorporation of the uncertainty associated with reproductive information into assessments would allow evaluation of the relative gain obtained by improved sampling of reproductive information relative to other inputs such as abundance surveys. Additionally, management strategy evaluations can be used to evaluate the risk to yield and stock abundance associated with imprecise information on reproductive biology.

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