Abstract—Predicting and understanding the dynamics of a population requires knowledge of vital rates such as survival, growth, and reproduction. However, these variables are influenced by individual behavior, and when managing exploited populations, it is now generally realized that knowledge of a species' behavior and life history strategies is required. However, predicting and understanding a response to novel conditions—such as increased fishing-induced mortality, changes in environmental conditions, or specific management strategies—also require knowing the endogenous or exogenous cues that induce phenotypic changes and knowing whether these behaviors and life history patterns are plastic. Although a wide variety of patterns of sex change have been observed in the wild, it is not known how the specific sex-change rule and cues that induce sex change affect stock dynamics. Using an individual based model, we examined the effect of the sex-change rule on the predicted stock dynamics, the effect of mating group size, and the performance of traditional spawning-per-recruit (SPR) measures in a protogynous stock. We considered four different patterns of sex change in which the probability of sex change is determined by 1) the absolute size of the individual, 2) the relative length of individuals at the mating site, 3) the frequency of smaller individuals at the mating site, and 4) expected reproductive success. All four patterns of sex change have distinct stock dynamics. Although each sex-change rule leads to the prediction that the stock will be sensitive to the size-selective fishing pattern and may crash if too many reproductive size classes are fished, the performance of traditional spawning-per-recruit measures, the fishing pattern that leads to the greatest yield, and the effect of mating group size all differ distinctly for the four sex-change rules. These results indicate that the management of individual species requires knowledge of whether sex change occurs, as well as an understanding of the endogenous or exogenous cues that induce sex change.

Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks

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Growth, survival, and reproduction all affect the dynamics of a population and its response to fishing and management (Quinn and Deriso, 1999; Haddon, 2001). However, these three key variables are influenced by many aspects of a species' biology, environment, and evolutionary history. There is an increasing realization that the management of populations requires an understanding of their behavior, life history strategies, and reproductive patterns (Sutherland, 1990; Huntsman and Schaaf, 1994; Collins et al., 1996; Greene et al., 1998; Sutherland, 1998; Beets and Friedlander, 1999; Coleman et al., 1999; Fulton et al., 1999; Kruuk et al., 1999; Constable et al., 2000; Cowen et al., 2000; Koeller et al., 2000; Fu et al., 2001; Apostolaki et al., 2002; Levin and Grimes, 2002). Although it is important to document the normal patterns of behavior and reproduction within a population, predicting and understanding a stock's response to novel conditions also requires knowledge of the degree of plasticity in behaviors that affect growth, survival, and reproduction, and the cues that induce phenotypic changes. Numerous examples exist of context- and condition-dependent behavior in fish

(e.g., Metcalfe et al., 1989; Snyder and Dingle, 1990; Schultz and Warner, 1991; Wainwright et al., 1991; Mittelbach et al., 1992; Nishibori and Kawata, 1993; Ridgeway and Shuter, 1994; Breden et al., 1995), and this kind of plasticity has the potential to affect the dynamics of a stock. For example, many commercially important species of fish change sex from female to male. Researchers have argued that this life history pattern will lead to different population dynamics and responses to fishing and management strategies than will the life history pattern of dioecious (separate-sex) species (e.g., Snyder and Dingle, 1990; Schultz and Warner, 1991; Wainwright et al., 1991; Nishibori and Kawata, 1993; Ridgeway and Shuter, 1994; Alonzo and Mangel, 2004). However, it is important to consider not only whether sex change occurs, but also how it occurs; whether plasticity in sex change exists and what cues determine sex change in an individual species.

A variety of patterns of sex change have been observed in the wild (Warner and Lejeune, 1985; Charnov, 1986; Shapiro, 1987; Charnov and Bull, 1989; Iwasa, 1990; Warner and Swearer, 1991; Lutnesky, 1994, 1996;

Kuwamura and Nakashima, 1998; Koeller et al., 2000; Nakashima et al., 2000). At one extreme, sex change may occur at a fixed size or age threshold. However, sex change is known in many species to be mediated by local factors such as population density, reproductive skew, sex ratio, and size distribution (Warner and Lejeune, 1985; Warner and Swearer, 1991; Lutnesky, 1994, 1996; Kuwamura and Nakashima, 1998; Koeller et al., 2000; Nakashima et al., 2000). In many sex-changing species, overlap exists between the sexes in size and age and this overlap indicates that sex change may also depend on individual experience and local conditions (Munoz and Warner, 2003). The pattern of sex change may have important implications for a species' response to fishing. For example, if the size at sex change is fixed, then the population sex ratio may be affected by size-selective fishing of males, resulting in sperm limitation and decreased larval production (Alonzo and Mangel, 2004). In contrast, if sex change is mediated at the level of the spawning group in single-male harems and mating group size remains the same, sex ratios are maintained if the largest female always changes sex. In such a case, larval production will be reduced only because of the decreased size distribution of the population due to fishing. However, if sex change is controlled by the reproductive skew in the group (e.g., the expected potential for reproduction as a male versus present fecundity as a female), then the largest individual might not change sex and the spawning group could be without a male (Munoz and Warner, 2003). This result would clearly lead to a much greater effect on the productivity of the stock. A detailed understanding of the factors determining sex change and the cascading effects on sperm production, fecundity, and sex ratio can be critical to predicting stock dynamics. Furthermore, most animals have "rules-of-thumb" which determine their behavior and reproduction. Although these rules will have evolved under normal conditions, in the presence of fishing or other human-induced disturbances, animals are likely to continue to use these behavioral rules on ecological time scales even if they no longer function to maximize reproduction.

Although previous fisheries models have examined sex change, a consensus does not exist regarding how sex change is predicted to affect stock dynamics. Some research has suggested that sex-changing stocks will be more sensitive to fishing and cannot be managed as if they were identical to separate-sex stocks (Bannerot et al., 1987; Punt et al., 1993; Huntsman and Schaaf, 1994; Coleman et al., 1996; Beets and Friedlander, 1999; Brule et al., 1999; Coleman et al., 1999; Armsworth, 2001; Fu et al., 2001). However, it has also been argued that, in the absence of sperm limitation, protogynous stocks should be less sensitive to size-selective fishing because female biomass and thus population fecundity should not decrease as much as in a dioecious population, making traditional management and theory conservative when applied to these species. In general, protogynous stocks have been predicted to be at risk of population crashes because of their potential for nonlin-

ear population dynamics in the presence of exploitation, yet there is no consensus regarding the importance of the exact pattern of sex change. For example, Armsworth (2001) examined protogynous stock dynamics when the probability of sex change was a fixed function of individual age and when the probability of sex change depended on the mean age of individuals in the population. He found that these two patterns of sex change had similar general dynamics and argued that management of a protogynous stock might not require knowledge of the precise pattern of sex change. In contrast, Huntsman and Schaaf (1994) and Coleman et al (1999) have argued that a consideration of the pattern of sex change can be important to managing stocks. But, past theory has generally focused on comparing fixed patterns of sex change with fully compensating reproductive patterns that maintain a fixed sex ratio or ratio of female to male biomass. However, a variety of patterns of sex change exist and there is no reason to believe that all species have evolved to exhibit full compensation under natural conditions, let alone under new situations. Thus, it is important to consider how specific sex change rules will affect the dynamics and management of protogynous stocks and whether knowledge of the cues that determine sex change will be important.

We (Alonzo and Mangel, 2004) developed a general modeling approach for examining the impact of reproductive behavior and life history pattern on stock dynamics. Using this approach, we then compared the dynamics of a protogynous population with fixed size at sex change and an otherwise identical dioecious species (Alonzo and Mangel, 2004). These analyses showed that although dioecious and protogynous stocks clearly have distinct dynamics, simple statements arguing that one life history pattern is more or less sensitive to fishing cannot be made. Protogynous stocks with fixed patterns of sex change were predicted to experience sperm limitation and lowered larval recruitment at high fishing pressure, whereas the dioecious stock was predicted to show a large drop in mean population size even at low fishing mortality, but was not predicted to experience lowered fertilization rates due to size-selective fishing. Both stocks were predicted to be sensitive to fishing pattern, but a fixed pattern of sex change was predicted to put a population at risk of crashing if all male size classes were fished even at relatively low fishing mortality. Finally, classic spawning-per-recruit (SPR) measures were not predicted to be good indicators of changes in the mean population size of protogynous stocks because they cannot indicate whether a population is experiencing sperm limitation and whether this limitation may lead to decreased population size or cause the stock to crash with small changes in fishing mortality. Although we found that whether or not a stock changes sex was important, that knowledge alone was not sufficient to understand and predict the response of the stock to fishing or management. We also found that sperm production and mating system were important variables affecting the probability that a population

would experience sperm limitation and would affect the performance of traditional spawning-per-recruit measures. However, we did not consider the possibility that size at sex change may be plastic and depend on local social conditions or relative rather than absolute size. Plastic sex change may allow a protogynous species to compensate for any effect of size-selective fishing on the sex ratio of the population, rendering its dynamics identical to the dynamics of a dioecious species. However, as described above, a wide variety of patterns of sex change have been observed in the wild and have been proposed to occur. Therefore, the exact pattern of sex change and cue driving phenotypic changes may lead to unique stock dynamics. In this study we apply the same general method we used previously (Alonzo and Mangel, 2004) to examine the effect of four different patterns of sex change (one fixed and three plastic) on the stock dynamics of a protogynous species.

Methods

We applied the same general method and individual-based population dynamic model as our previous study (Alonzo and Mangel, 2004). However, we now included the effect of four different patterns of sex change on the stock dynamics and performance of spawning-per-recruit measures in a protogynous species. Individuals vary in age, size, sex, and location (i.e. mating site). We assumed annual time periods and determined individual survival, size, and reproduction as described below. We simulated 100 years prior to examining the impact of fishing on stock dynamics and then simulated 100 more years in the presence of fishing with a constant mean fishing-induced mortality. This allowed the population to reach a stable age, sex, and size distribution prior to fishing which is independent of initial conditions. Because a number of elements of the model are stochastic, we examined 20 simulations for each scenario and set of parameter values, which was more than sufficient in all cases to lead to low variability in the key measures of interest.

Fishing and adult survival

We assume age and size do not affect natural adult mortality, μ_A, and that adult mortality is density-independent. The fishery is size selective; if L represents fish size, F annual fishing mortality, L_f the size at which there is 50% chance an individual of that size will be taken, and r the steepness of the selectivity pattern, the fishing selectivity per size class $s(L)$ is given by

$$s(L) = \frac{1}{1 + \exp\left(-r(L - L_f)\right)} \qquad (1)$$

and adult annual survival is

$$\sigma(L) = \exp\left(-\mu_A - Fs(L)\right). \qquad (2)$$

Population dynamics

The number of larvae that enter the population is determined by larval survival and the total production of fertilized eggs $P(t)$, which is determined by total fecundity and fertility within each mating site as described below. Larval survival is assumed to have both density-independent and density-dependent components (e.g., Cowen et al., 2000; Sale, 2002), and we use a Beverton-Holt recruitment function (Quinn and Deriso, 1999; Jennings et al., 2001) to calculate larval survival . The number of larvae surviving to recruit in any year t, $N_0(t)$, is given by

$$N_0(t) = (\alpha P(t)) / (1 + \beta P(t))$$

$$\text{if } (\alpha P(t)) / (1 + \beta P(t)) + \sum_{a=1} N_a(t) \le N_{\max}$$

$$\qquad\qquad (3)$$

$$N_0(t) = \max\left(0, N_{\max} - \sum_{a=1} N_a(t)\right)$$

$$\text{if } (\alpha P(t)) / (1 + \beta P(t)) + \sum_{a=1} N_a(t) > N_{\max},$$

where α gives density-independent survival, β determines the strength of the density-dependence in the larval phase, and N_{max} represents the maximum population size. We assume that the population is open between mating sites, a single larval pool exists, larval recruitment is random among mating sites, and there is no emigration to or immigration from outside populations.

Growth dynamics

Larvae that survive to recruit begin at size L_0 and growth is assumed to be deterministic and independent of sex or reproductive status. We calculate growth between age classes using a discrete time version of the von Bertalanffy growth equation (Beverton, 1987, 1992) where L_{inf} represents the asymptotic size and k is the growth rate. Then an individual of length $L(t)$ at time t will grow in the next time period to size $L(t+1)$:

$$L(t+1) = L_{inf}\left(1 - \exp(-k)\right) + L(t)\exp(-k). \qquad (4)$$

Mating system

As in our previous model, we assume that reproduction occurs at the level of the mating group, and we examine the effect of varying mating group size and the number of mating sites. Juveniles and adults are assumed to exhibit site fidelity and larvae settle randomly among mating sites. The carrying capacity of the population is split equally among the mating sites and the total capacity of all mating sites exceeds the maximum population size in the absence of fishing as determined by

adult mortality and the recruitment function. As before (Alonzo and Mangel, 2004), we examine the following three cases: 1) the entire population mates at one site (1 mating site with up to 1000 individuals); 2) a few large mating groups exist (10 sites with a maximum of 100 individuals per site); and 3) many small mating aggregations exist (20 mating sites with a maximum of 50 individuals per site). We assume that within a mating site, individuals mate in proportion to their fertility and fecundity and that males that are large enough to change sex have a chance of reproducing that is proportional to their fertility and thus a large male reproductive advantage exists. This is equivalent to assuming that females exhibit a mate choice threshold (Janetos, 1980) that has evolved with the size at pattern of sex change and that male fertilization success is proportional to fertility.

Reproduction

We assume female fecundity $E(L)$ and male sperm production $S(L)$ can be represented by the allometric relationships $E(L)=aL^b$ and $S(L)=cL^b$ respectively where a, b and c are constants. We assume that at any body length males produce 1000 times more sperm than females produce eggs. This leads to the realistic pattern that (in the absence of fishing) fertilization rates are high and that multiple males are needed to fertilize all the eggs produced by females. We calculate the average expected fertilization rate per mating site based on the total production of sperm and eggs at the site, where S represents the number of sperm released (in millions) and E the number of eggs released at each mating site. The proportion of eggs fertilized per mating site p_F is given by

$$P_F = \frac{S}{1+(\kappa E + \chi)S},\qquad(5)$$

where κ and χ are constants fitted to data. The proportion of eggs fertilized (p_F) depends on both total sperm production (S) and egg production (E). If sperm production is very high in relation to egg production, fertilization rates will be at or near 100%. However, if total sperm production (S) decreases and egg production remains the same, fertilization rates will decrease. Similarly, as egg production (E) increases in relation to total sperm production (S) fertilization rates will decrease (see Fig. 2, Alonzo and Mangel, 2004). The number of eggs fertilized per group is $p_F E$ and the total production of fertilized eggs $P(t)$ is the sum of the number of eggs fertilized in all mating groups. For more details on the fertilization function and individual sperm production see Alonzo and Mangel (2004).

Patterns of sex change

We examine four possible patterns of sex change, determined by absolute or relative size of the individual. Although a variety of other possibilities exist, these examples represent four plausible patterns that differ in the cues or mechanisms that induce sex change, the degree of compensation or plasticity assumed, and encompass the diversity that has been observed and hypothesized for a variety of sex-changing fish populations (Helfman, 1997).

Rule 1: Fixed   For the first sex-change rule, we assume that the probability of sex change $p_C(L)$ is determined by the absolute length of the individual and is

$$p_c(L) = \frac{1}{1+\exp\left(-\rho(L-L_c)\right)},\qquad(6)$$

where L_C represents the size at which 50% of mature females change sex and ρ is a constant that determines the steepness of the probability function. With this sex change rule, we also assume that the probability an individual matures $p_M(L)$ is determined by absolute size. Once an individual matures, she remains female until sex change. L_M represents the length at which 50% of juveniles are expected to mature.

$$p_M(L) = \frac{1}{1+\exp\left(-q(L-L_M)\right)},\qquad(7)$$

where q determines the steepness of the probability function and where $L_C > L_M$.

Rule 2: Relative size   For the second sex change rule, the mean size of all individuals in the mating group determines the probability of sex change for an individual. First, we find the mean size of all individuals at each mating site. We let L_i represent the mean size in the mating site i. Then the probability of sex change for an individual of length L is

$$p_c(L) = \frac{1}{1+\exp\left(-\rho\left(L-(L_i+\Delta L_c)\right)\right)},\qquad(8)$$

where ΔL_C represents the difference from the mean at which the probability of sex change is 0.5. For these analyses, we also assumed that the probability an individual matures also depends on the mean size of individuals at the mating site. Then the probability of maturity is

$$p_M(L) = \frac{1}{1+\exp\left(-q\left(L-(L_i+\Delta L_M)\right)\right)},\qquad(9)$$

where ΔL_M represents the difference from the population mean at which the probability an individual will mature is 0.5.

Rule 3: Relative frequency   Sex change may also be induced by the social conditions at the mating site. For example, sex change may depend on the frequency of

other mature individuals or the frequency of smaller individuals. We examine the case where sex change depends on the frequency of smaller mature individuals. For each mature female, we find the frequency of mature individuals at the same mating site that are smaller. We let F_i represent the frequency of mature individuals that are smaller than the mature female and F_C represents the frequency at which 50% of the individuals are expected to change sex. Then the probability of sex change is

$$p_c(L) = \frac{1}{1 + \exp\left(-\rho(F_i - F_c)\right)}. \tag{10}$$

The probability of maturing depends on the frequency of smaller individuals. We let f_i represent the frequency of all smaller individuals at mating site i and f_M represent the frequency at which there is a 50% probability of an individual maturing. Then the probability of maturing is

$$p_M(L) = \frac{1}{1 + \exp\left(-q(f_i - f_M)\right)}. \tag{11}$$

Rule 4: Reproductive success   Finally, we consider the case where sex change occurs when an individual's size-dependent expected reproductive success is greater as a male than as a female (Charnov, 1982). This pattern of sex change has been proposed to explain the observation that individual variation exists in size at sex change and that it is not always the largest individual in a group that changes sex (Munoz and Warner, 2003). We assume that a fish will change sex when its expected egg production at its current length ($E(L)=aL^b$ as given above) is exceeded by its expected paternity at the mating site which is given by the total egg production of all other females at the site multiplied by the focal individual's relative sperm production. This value is given by expected fertility $S(L)$ divided by the total sperm production (by all males at the site plus their own expected fertility) at the same mating site. We further assume that sex change occurs once a year in rank order from the largest to smallest female at the site. (For this scenario we assumed that the probability of maturing depends on absolute size as in Equation 7.) However, we still assume that individuals can only change sex once during their lifetime and only mature females can change sex. Thus, mature females change sex when their current expected fertilization success as a male is greater than their current expected fecundity as a female.

Measures of spawning stock biomass per recruit

We examine the same spawning-per-recruit measures as in our previous paper (Alonzo and Mangel, 2004) and compare the results of the patterns of sex change considered here with one another and with a hypothetical dioecious species, where sex is determined stochastically at birth and the primary sex ratio is fixed. We compute the total spawning stock biomass per recruit starting from the beginning of fishing for the next 50 years. We use the generally recognized pattern that fish wet weight tends to be approximately proportional to the cube of fish length (Gunderson, 1997) to convert fish length, L, into relative biomass, $B(L)\sim L^3$. Then we calculate total, female, and male spawning stock biomass per recruit (SSBR). We also keep track of the total fecundity (egg production per recruit), fertility (sperm production per recruit), and eggs fertilized per recruit.

Parameter values

We use parameters based on previous research (Warner, 1975; Cowen, 1985; Cowen, 1990) on California sheephead *(Labridae, Semicossyphus pulcher)*, a commercially important sex-changing fish, to provide evolutionarily and ecologically reasonable parameters for the model. Although the growth, survival, and reproduction of this species have been studied, less is known about the factors that induce sex change and mating behavior. In this species, sex change occurs at approximately 30 cm, although the exact pattern varies among populations (Warner, 1975; Cowen, 1990). It is not known whether sex change is fixed or socially mediated. For the first sex-change rule, we assume that individuals have a 50% chance of maturing (L_m) at 20 cm (the mean size of maturity observed in natural populations) and of changing sex at (L_c) 30 cm. This leads to a sex ratio of 2/3 mature females to 1/3 males on average and a mean length of 20 cm in the absence of fishing as is observed in the wild. For consistency, we also assume for the second sex-change rule, that individuals have a 50% chance of changing sex at 10cm (ΔL_c=10) above the mean size and have a 50% chance of maturing at the mean size in the mating site (ΔL_m=0). Similarly, for the third rule, the frequency of smaller mature individuals at which there is a 50% of sex change is assumed to be 0.67 and when 50% of all individuals are smaller, an individual will have a 0.5 probability of maturing. Therefore in the absence of fishing all four sex change rules lead to the same maturity and sex-change patterns as a function of age and size. For more information on the parameter values considered here, see Table 1.

Individual-based simulations are computationally very intensive. As a result, it was not feasible to explore a wide range of values for all parameters. Furthermore, because growth, mortality, reproduction, maturity, and sex change are coevolved characters within any species, it does not make sense in this context to vary them independently. Instead, we used estimates from California sheephead for as many parameters as possible (mortality, growth, fecundity, size at maturity, and sex change) and when necessary from a closely related species (fertilization rate). We then focused on exploring the effect, for this species, of varying the sex-change rule and fishing pattern while all other parameters remained the same. Our focus was on determining the impact of the sex change rule on the predicted stock

Table 1

The parameter values used in the model were based on available data for California sheephead (*Semicossyphus pulcher*). See text for details.

Parameter	Parameter values	Definition and source
Growth		
k	0.05	Growth rate (based on Cowen, 1990)
L_{inf}	90 cm	Asymptotic size (based on Cowen, 1990)
L_0	8 cm	Larval size at recruitment
Population		
N_{max}	1000	Maximum population size
μ_A	0.35	Adult mortality (based on Cowen, 1990)
α	0.0001	Density-independent larval mortality
β	$\alpha/(1-\exp(-\mu_A))\,N_{max}$ (3.33×10^{-7})	Larval recruitment function parameter (see text)
Fishing		
r	1 (0.1)	Steepness of selectivity curve
L_f	30 (25, 35)	Length at which 50% chance a fish will be removed
F	0–3	Fishing mortality
Reproduction		
a	7.04	Constant in the fecundity relationship (Warner, 1975)
b	2.95	Exponent in the allometric relationship (Warner, 1975)
c	$10^{-3}a$	Constant in the sperm production function (measured in millions of sperm)
κ	0.000003	Slope of fertilization function parameter
χ	0.09	Intercept of fertilization function parameter (based on Peterson et al., 2001) see text for details
Rule 1		
L_c	30 cm	Length at which 50% of fish change sex
ρ	1	Shape parameter in the sex-change function
L_m	20 cm	Length at which 50% of fish mature
q	1	Shape parameter in the maturity function
Rule 2		
ΔL_c	10 cm	Difference from the mean size at which $p_c(L)= 0.5$
ρ	1	Shape parameter in the sex change function
ΔL_m	0 cm	Difference from the mean size at which $p_M(L)= 0.5$
q	1	Shape parameter in the maturity function
Rule 3		
F_c	0.67	Frequency of smaller mature individuals where $p_c(L)=0.5$
ρ	50	Shape parameter in the sex-change function
F_m	0.50	Frequency of smaller individuals at which $p_M(L)=0.5$
q	50	Shape parameter in the maturity function
Rule 4		No additional parameters required

dynamics rather than on exploring all possible parameter combinations. However, it would certainly be useful in the future to examine the same question using parameter estimates based on other commercially exploited species that change sex.
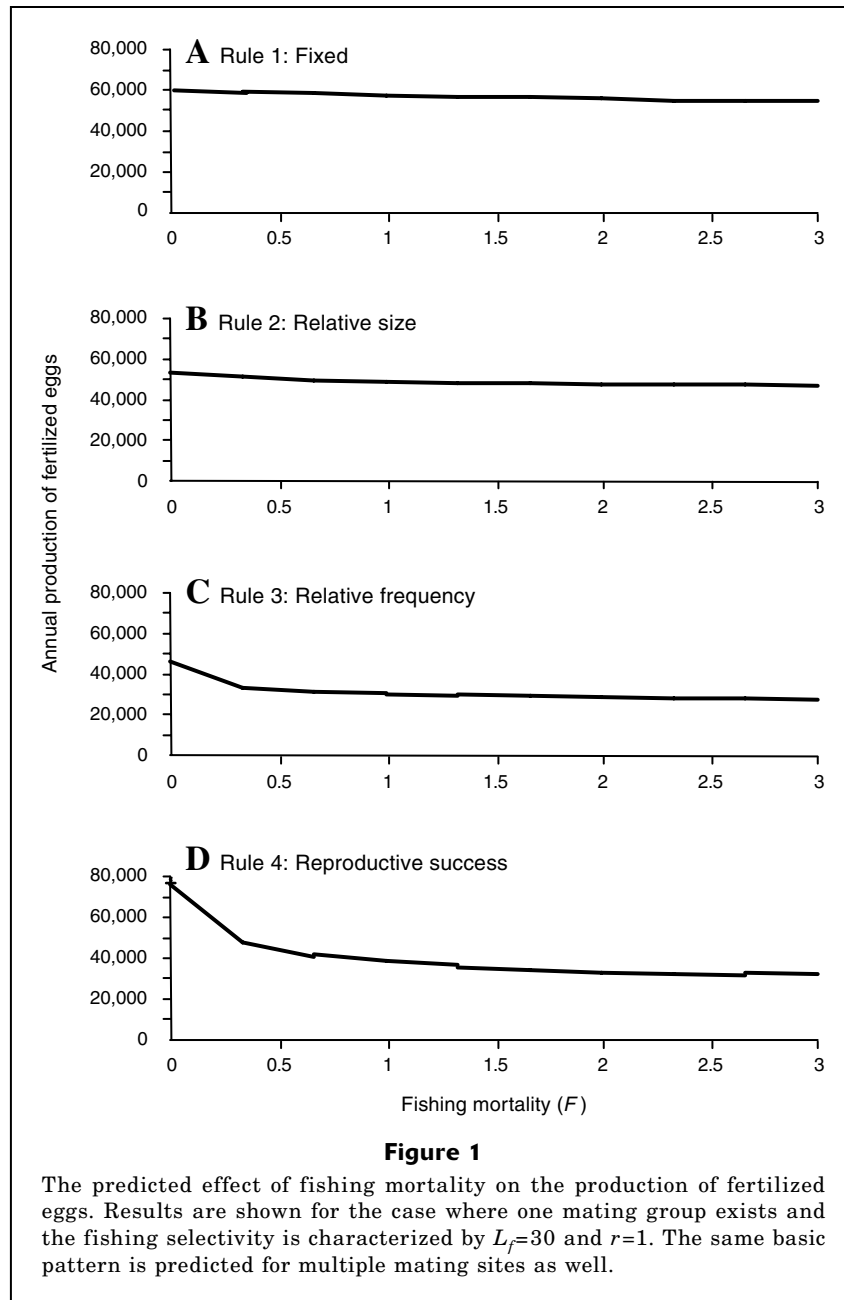
Results

We present the average across simulations of the mean population measures of the last 50 years for each simulation. The variation around the mean in all measures considered is hundredths of a percent of the mean or less. For the spawning-per-recruit (SPR) measures we give the mean value across the first 50 years of fishing

to ensure that the entire cohort under consideration had died before the end of the simulation. Parameter values used are given in Table 1

General dynamics

In all cases, size-selective fishing is predicted to decrease population size and decrease the mean length of fish in the population. Although all scenarios are predicted to lead to the same change in average fish length, the effect of fishing on predicted population size and the mechanisms leading to changes in population size differ between the four sex-change rules (Figs. 1 and 2, Table 2). The largest differences occur between the fixed rule and the three plastic patterns of sex change. How-

Figure 1

The predicted effect of fishing mortality on the production of fertilized eggs. Results are shown for the case where one mating group exists and the fishing selectivity is characterized by L_f=30 and r=1. The same basic pattern is predicted for multiple mating sites as well.
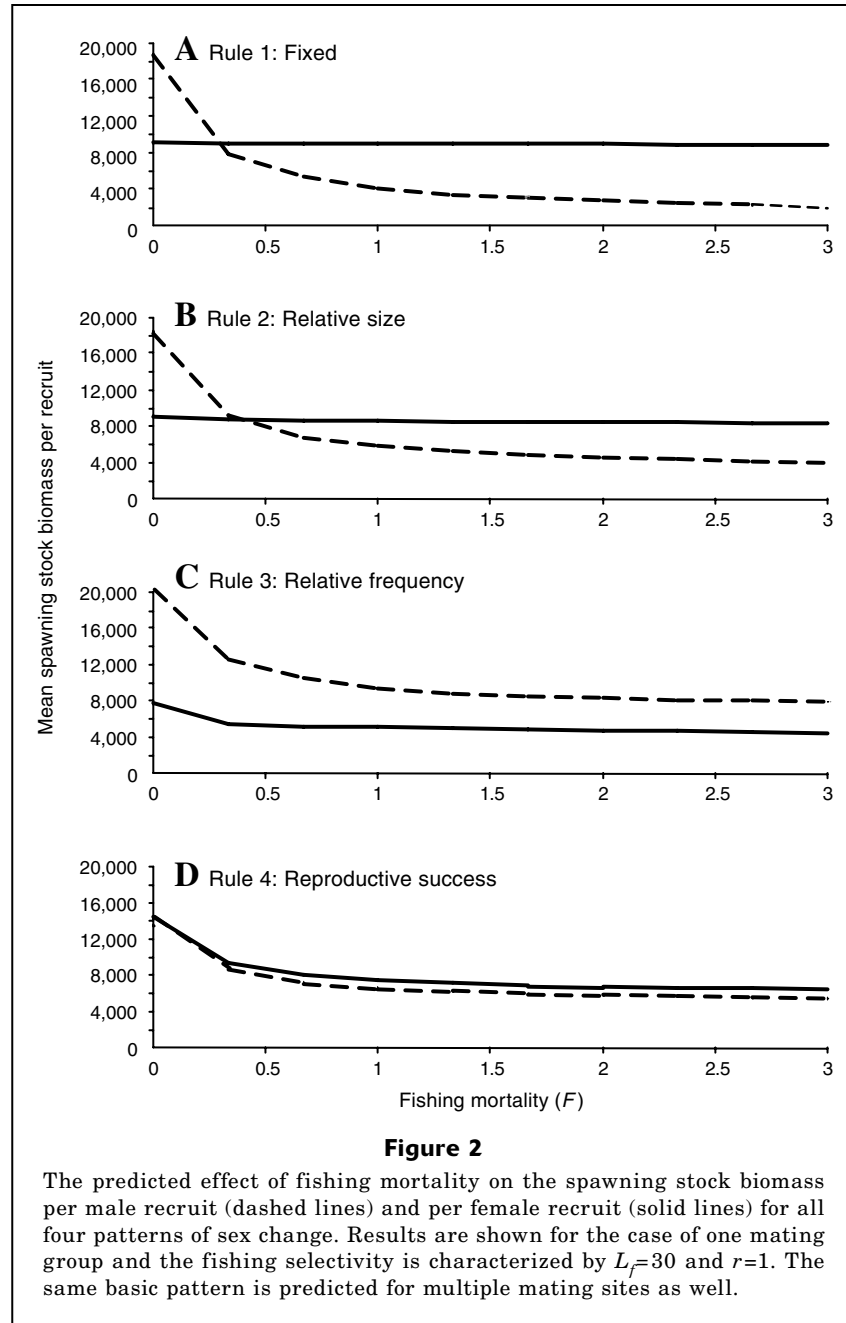
ever, the exact pattern of sex change has an important and qualitative effect on the predicted stock dynamics (Table 2). All three plastic patterns of sex change are predicted to show lower sperm limitation and higher fertilization rates in the presence of fishing than the fixed pattern of sex change (Table 2). However, associated with plastic sex change is also a greater predicted drop in egg production (total and fertilized) and mean population size than when the effect of size on the probability of sex change is fixed (Fig. 1, Table 2). This drop in egg production and mean population size occurs because female biomass is predicted to decrease as a result of the combination of fishing on larger individuals and smaller

sizes at sex change (Fig. 2). The basic patterns are the same for the case with multiple mating sites. Most of the significant reductions in stock size are predicted at high fishing mortality. However, it is important to remember that we have assumed that the stock is very resilient (Table 1), and our focus is on the differences among sex-change rules and fishing patterns rather than on absolute fishing mortality.

The effect of mating group size

Although mating group size is predicted to have an effect in most cases on the stock dynamics of the population,

Figure 2

The predicted effect of fishing mortality on the spawning stock biomass per male recruit (dashed lines) and per female recruit (solid lines) for all four patterns of sex change. Results are shown for the case of one mating group and the fishing selectivity is characterized by $L_f=30$ and $r=1$. The same basic pattern is predicted for multiple mating sites as well.

the strongest effect is predicted when size at sex change is fixed or determined by the frequency of small fish in the population (Fig. 3, A and C). When the size at sex change is fixed, populations are predicted to crash when mating sites are very small (Fig. 3A). In the case where size at sex change is determined by expected reproductive success, group size is predicted to have no effect on the relative production of eggs and mean population size (Fig. 3D). However, for all the other rules of sex change considered, smaller mating sites are predicted to experience sperm limitation in the presence of fishing, leading to a decrease in the relative production of fertilized

eggs and a decrease in mean population size (Fig. 3). However, unlike in the case of fixed size at sex change, the smaller mating groups (20 mating sites with up to 50 individuals per site) are stable both in the presence and absence of fishing and are not predicted to collapse for most fishing patterns.

Sensitivity to fishing pattern

Rule 1 The size-selective pattern of the fishery has a large effect on the predicted stock dynamics when the size at sex change is fixed. When the selectivity of the

Table 2

A comparison of stock dynamics for four sex-change rules. Results are reported for the situation where the fishing selectivity pattern and the probability of sex change are both centered at the same size (L_f=30). These results assume a near knife-edge selectivity (r=1) and that one mating site exists. Numbers given are for the predicted relative change as a result of fishing (when F=3 compared to F=0). SSBR = spawning stock biomass per recruit.
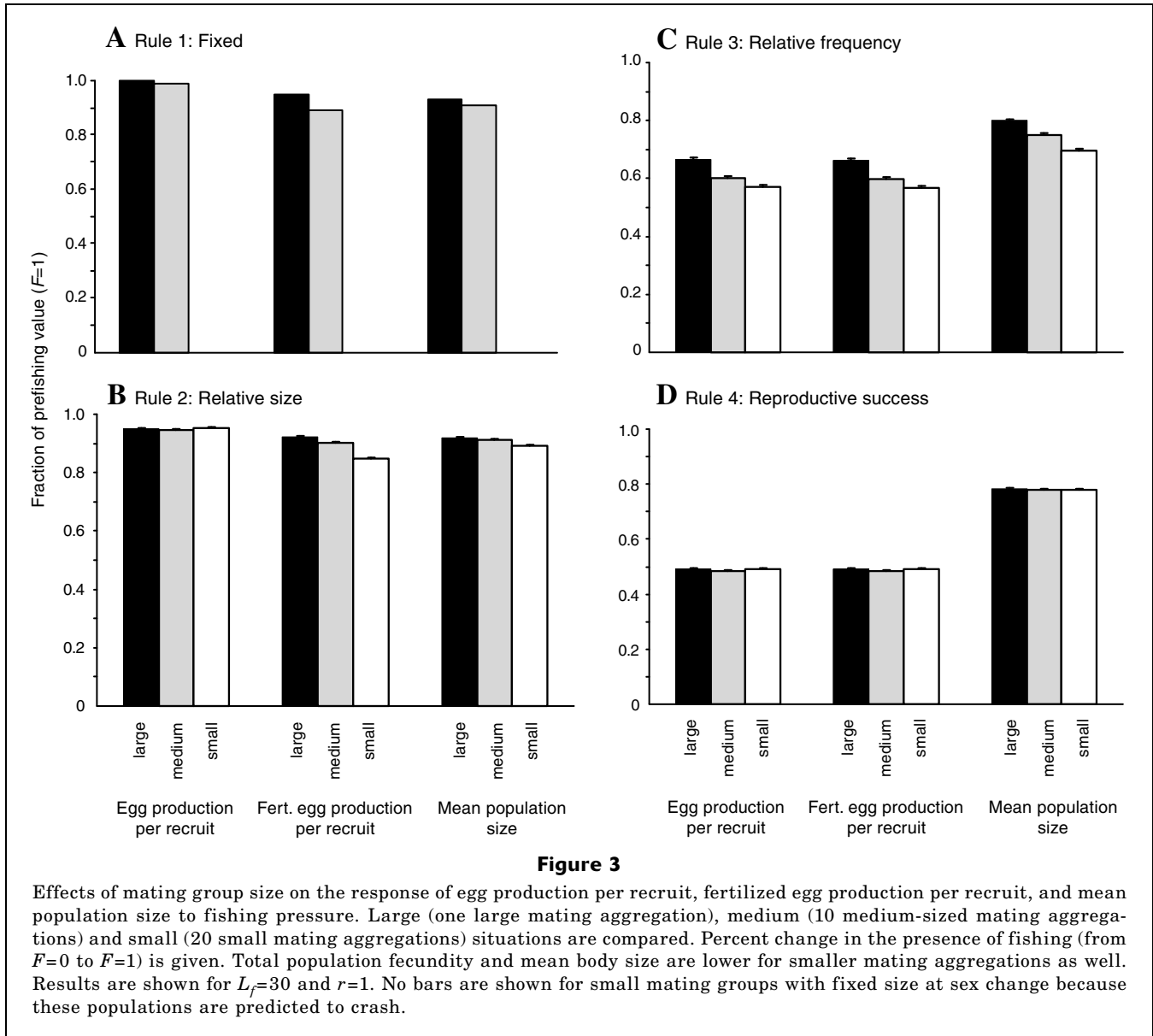
	Rule 1: Fixed	Rule 2: Relative size	Rule 3: Relative frequency	Rule 4: Reproductive success
Mean population size	90%	90%	73%	72%
Total SSBR	40%	45%	44%	39%
Male SSBR	11%	22%	39%	39%
Female SSBR	98%	92%	58%	39%
Sex ratio	0.67 → 0.92	0.67 → 0.84	No change	0.8 → 0.66
Mean size	88%	88%	88%	88%
Sperm production	11%	23%	40%	40%
Egg production	98%	93%	59%	41%
Fertilized egg production	88%	86%	59%	41%

fishery is centered below the mean size at sex change (L_f=25, r=1), the stock was predicted to crash at high fishing mortality (F≥1, Fig. 4A). Furthermore, when the selectivity pattern was not steep (L_f=30, r=0.1), the population was always predicted to crash even at low fishing mortality (and thus this case is not shown in Figs. 4A–6A). When the steepness of the fishery's selectivity changes, the size range over which fish are targeted also changes. Thus, smaller and younger fish are removed by the fishery when r=0.1 and hence a greater number of age classes are affected by fishing. At an extreme, fishing mortality could be high enough that all of the individuals in any size classes targeted by the fishery are removed. As a result, although the steepness of the selectivity function only affects the spread of the function mathematically, it has the biological effect of decreasing the size at which fish experience fishing mortality and can have a large effect on the size and age distribution of the population. In contrast, when the fishery's selectivity is steep (r=1) and only fish at or above the mean size at sex change (L_f≥30) are targeted, the effect of fishing on the population is predicted to be much less (Fig. 4A). Independent of the selectivity pattern, the population sex ratio is predicted to be more female-biased in the presence of fishing than in the absence of fishing. The lower the mean size removed by the fishery, the greater the predicted change in population sex ratio as a result of fishing (Fig. 5A). For situations in which the stock is not predicted to crash (i.e., L_f≥30 and r=1), yield is predicted to increase with diminishing returns with fishing mortality (Fig. 6A), catch is not predicted to decline with increased fishing mortality (at least up to F=3), and steep size-selective fishing patterns with lower size thresholds are predicted to lead to more yield (Fig. 6A).

Rule 2   When sex change is determined by the mean size of individuals in the mating site and the size-selec-

tivity is weak (r=0.1), the population is predicted to crash when F≥1.67 (Fig. 4B). This crash occurs because individuals do not escape fishing mortality even at small sizes. However, unlike when sex change is fixed (Fig. 4A), the population is predicted not to crash when the size selected by the fishery is less than the mean size at sex change in the absence of fishing (L_f=25, Fig. 4B). The larger the mean size selected by the fishery, the smaller the predicted effect of fishing on the mean population size and the population sex ratio (Figs. 4B and 5B). Although catch is predicted to increase with diminishing returns as fishing mortality increases from zero to three, the difference between the size-selectivity patterns is predicted to decrease and yield will be greater annually if larger fish are targeted (Fig. 6B).

Rule 3   As above, when the probability of sex change depends on the relative frequency of smaller mature individuals, the population is predicted to crash whenever size-selectivity is weak because fish do not escape fishing even when small (r=0.1, Fig. 4C). Although the population is predicted not to crash when the size targeted by the fishery is less than the mean size at sex change in the absence of fishing (L_f=25, Fig. 4C), this fishing pattern is predicted to lead to a large decrease in mean population size and a marked decrease in population sex ratio (Figs. 4C and 5C). In contrast fishing selectivity that is centered at or above the mean size of sex change in the absence of fishing (L_f=30 and L_f=35) is predicted to lead to a weaker effect on mean population size and to almost no effect on the population sex ratio (Figs. 4C and 5C). However, in contrast to the two scenarios described above this pattern of sex change leads to the prediction that targeting fish at or larger than the normal mean size of sex change (L_f=30 and r=1) will lead to the greatest annual yield over time for most fishing mortalities (Fig. 6C).

Figure 3

Effects of mating group size on the response of egg production per recruit, fertilized egg production per recruit, and mean population size to fishing pressure. Large (one large mating aggregation), medium (10 medium-sized mating aggregations) and small (20 small mating aggregations) situations are compared. Percent change in the presence of fishing (from $F=0$ to $F=1$) is given. Total population fecundity and mean body size are lower for smaller mating aggregations as well. Results are shown for $L_f=30$ and $r=1$. No bars are shown for small mating groups with fixed size at sex change because these populations are predicted to crash.

Rule 4 As with all of the other patterns of sex change, populations with sex change based on expected reproductive success are predicted to crash whenever small fish experience fishing mortality ($r=0.1$, Fig. 4D). Furthermore, as with the other two plastic sex change rules, populations are predicted not to crash when fish below the normal mean size at sex change are included in the fishery because the population can compensate with smaller sizes at sex change in the presence of fishing (Fig. 4D). Although only small differences among fishing patterns are predicted in the mean population sex ratio, the effect on the population size is predicted to be greatest when many size classes are fished, and large differences are predicted between the fishing patterns in mean population size (Fig. 5D). Finally, in the scenario of sex change based on expected reproductive success,

the fishing pattern predicted to lead to the greatest catch is to target only fish above the normal mean size at sex change ($L_f=35$, Fig. 6D).

In summary, fishing is always predicted to decrease total production of fertilized eggs and mean population size. However, the strength of the effect depends both on fishing selectivity and the pattern of sex change (see above and Figs. 4–6). Although populations with fixed patterns of sex change are predicted to crash in the presence of fishing below the mean size at sex change, plastic patterns of sex change are predicted to lead to more resilience since these populations can compensate for the removal of large males more effectively. However, all scenarios are predicted to crash in the presence of fishing across a broad range of size classes (when $r=0.1$) even in completely compensatory patterns of sex change.
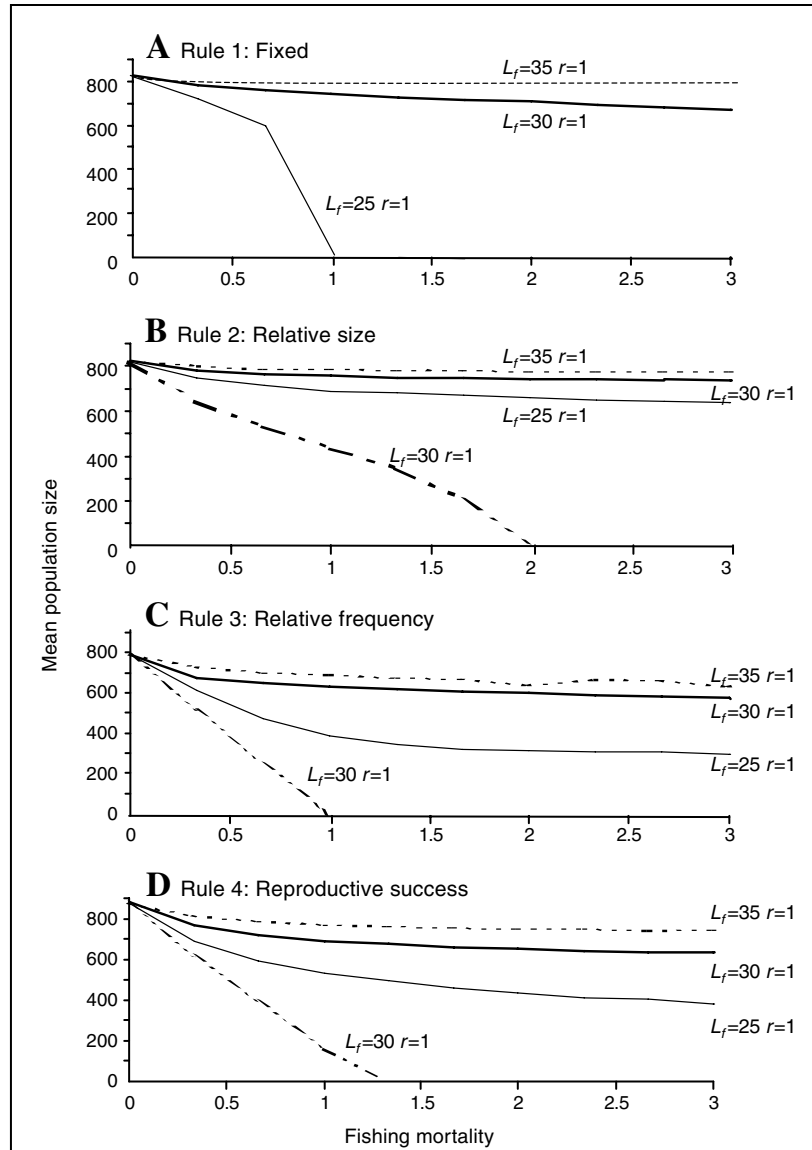
Figure 4

The effect of size-selective fishing on the predicted mean population size for all four patterns of sex change. We present results for a sex-changing stock with one mating site. Means across 20 simulations are given. For details see text. The same basic patterns are predicted with multiple mating sites. A line is not shown in panel A (when sex change is fixed) where $L_f=30$ and r=0.1 because the population is predicted to crash at any fishing mortality in this scenario.

Yet, the exact response depends greatly on the specific pattern of sex change. For example, the population sex ratio is not predicted to change much in the presence of fishing when sex change is based on expected reproductive success and fishing pattern has little effect on the sex ratio (Fig. 5). However, when sex change is based on expected reproductive success, the annual yield is greater for fishing patterns with larger size thresholds (Fig. 6). In contrast, when sex change is determined by the mean size of individuals at the mating site, sex ratio is predicted to increase with fishing and increase more when smaller size classes are fished. However, for this pattern of sex change, the smallest size threshold is also predicted to lead to the largest yield of the fishery, although as fishing mortality increases the difference between fishing patterns with differing size thresholds decreases. Therefore, the fishing pattern that will produce optimal yield will depend on the exact pattern of sex change (Fig. 6).
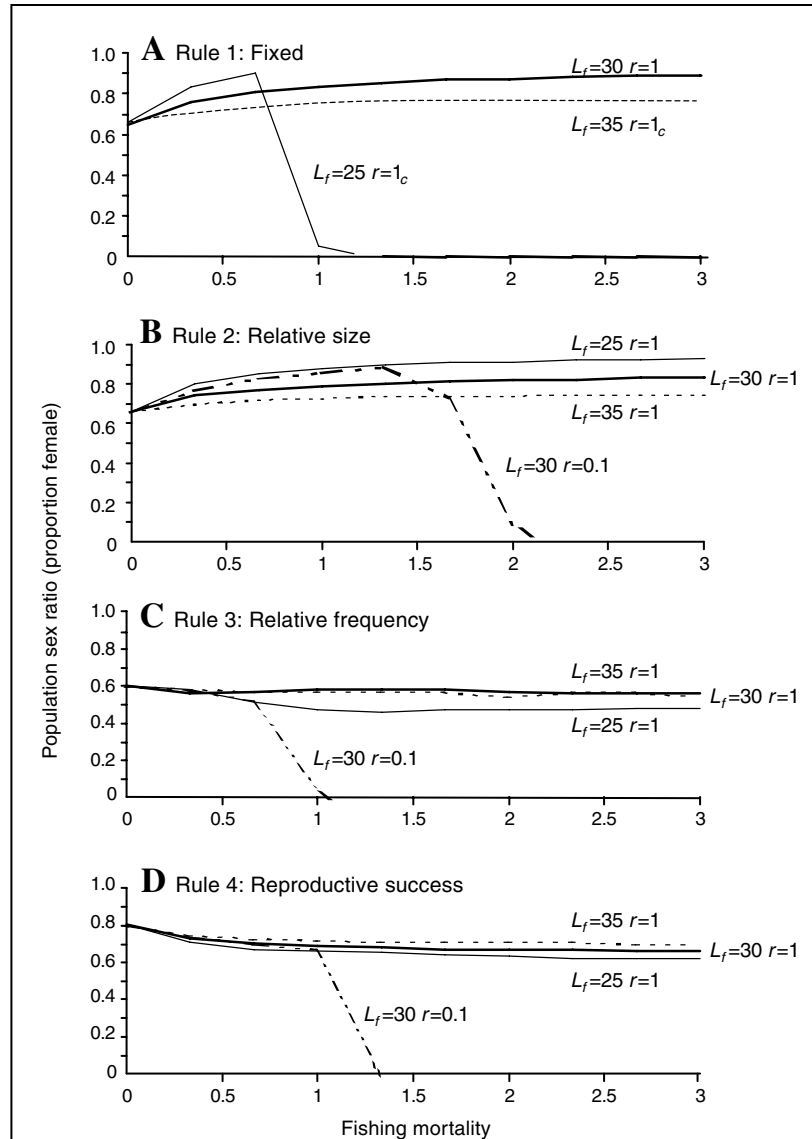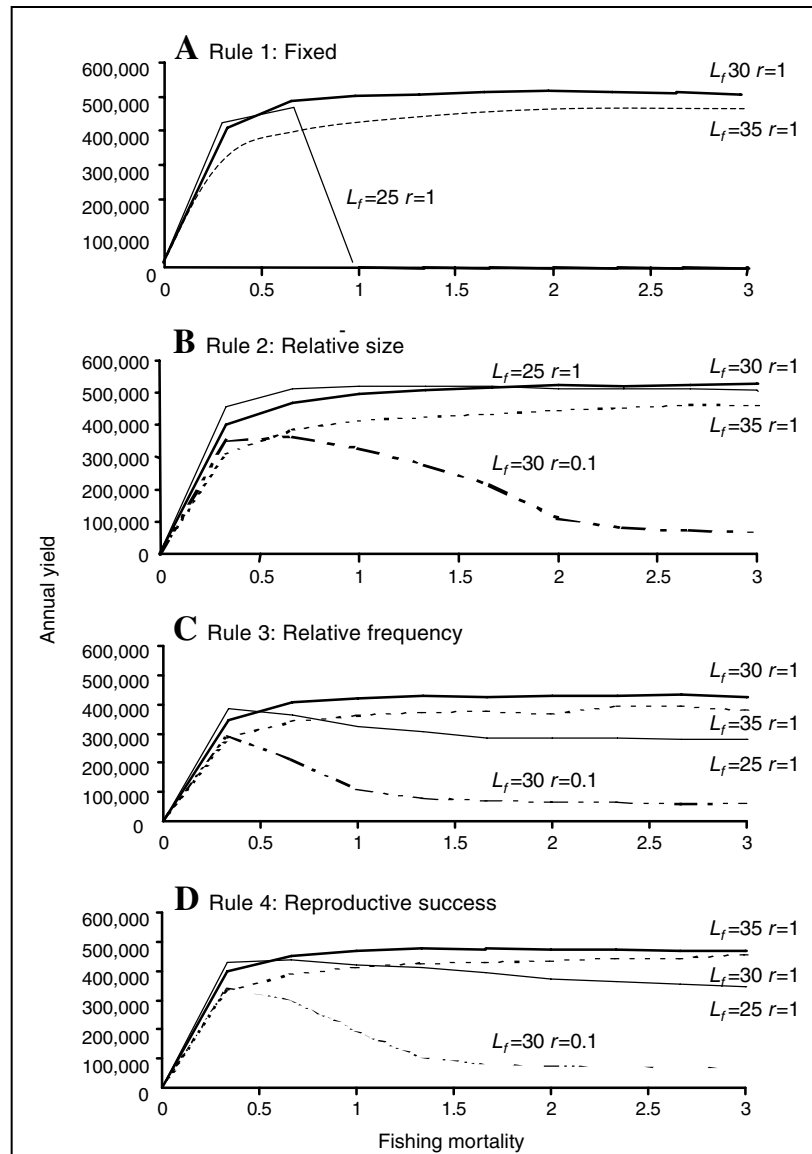
Figure 5

The effect of size-selective fishing on the predicted population sex ratio for all four patterns of sex change. We present results for a sex-changing stock with one mating site. Means across 20 simulations are given. For details see text. The same basic patterns are predicted with multiple mating sites. A line is not shown in panel A (when sex change is fixed) where L_f=30 and r=0.1 because the population is predicted to crash at any fishing mortality in this scenario.

Spawning-per-recruit (SPR) measures and a comparison of protogynous and dioecious stocks

Our previous results (Alonzo and Mangel, 2004) have shown that whether species change sex or are dioecious is predicted to have dramatic effects on both the stock dynamics and performance of classic SPR measures. However, our results show that the exact pattern of sex chang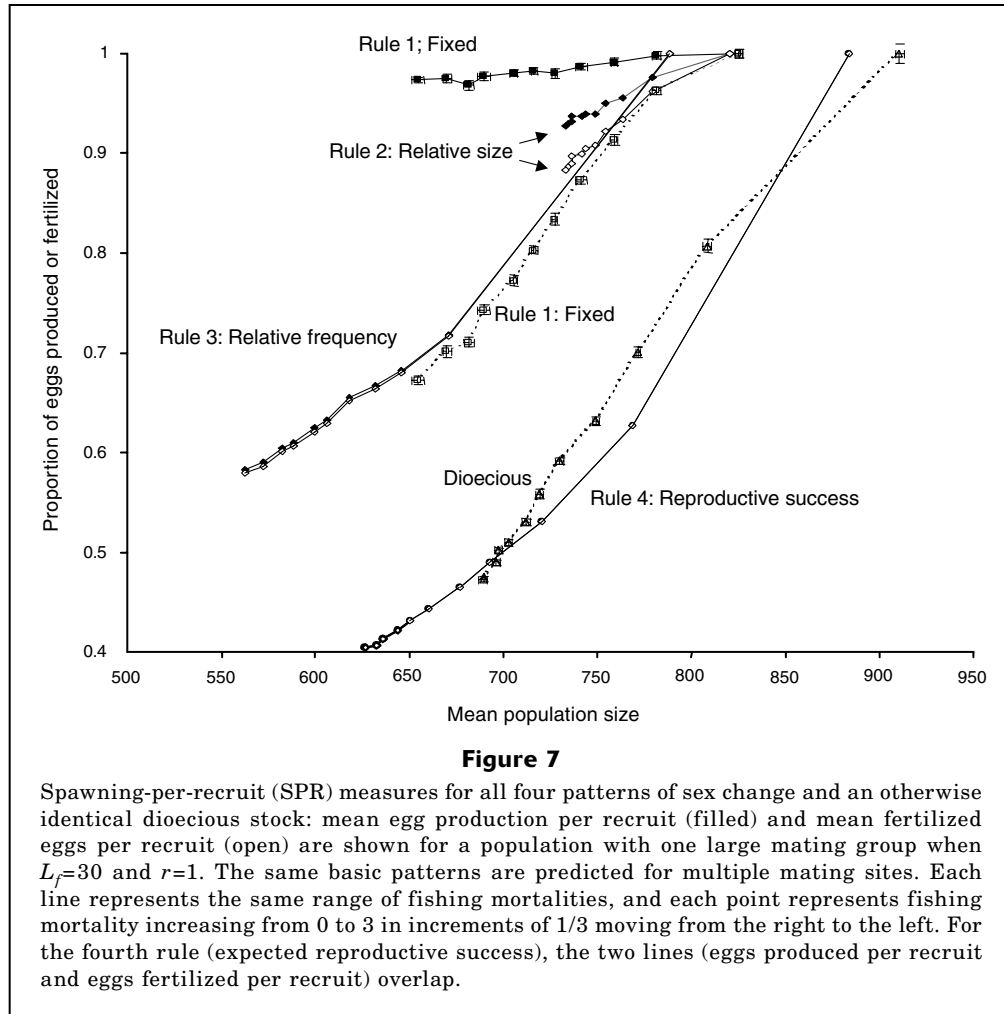e, and not just whether the pattern is plastic or fixed, can have a strong effect on these measures as well (Fig. 7). Because of the population dynamics of the model, all the scenarios represented in the present study show a great resiliency to fishing. Hence, the predicted changes in stock size are all above the common threshold of allowing a reduction of spawning per recruit measures to 40% of their values in the unfished condition. However, our aim is not determine if this population is overfished. Instead, it is to determine whether classic

Figure 6

The effect of size-selective fishing on the predicted annual yield for all four patterns of sex change. We present results for a sex-changing stock with one mating site. Means across 20 simulations are given. For details see text. The same basic patterns are predicted with multiple mating sites. A line is not shown in panel A (when sex change is fixed) where L_f=30 and r=0.1 because the population is predicted to crash at any fishing mortality in this scenario.

spawning per recruit measures based on egg production or fecundity could accurately assess the status of sex-changing stocks. Although the fixed pattern of sex change is predicted to show the greatest difference between egg production per recruit and fertilized eggs produced per recruit, each population shows deviations between egg production and the production of fertilized eggs. Thus egg production alone cannot tell us how the population is being affected by fishing and classic

SPR measures based on population fecundity may be misleading for sex-changing stocks in cases where the sex-change rule is not completely compensatory (rules 1–3). It is also interesting to ask whether consistent differences exist (as has been suggested) in the resiliency of sex-changing stocks, compared to stocks with separate sexes. Our results indicate that sex change based on expected reproductive success is predicted to have very similar dynamics to the dioecious population,

Figure 7

Spawning-per-recruit (SPR) measures for all four patterns of sex change and an otherwise identical dioecious stock: mean egg production per recruit (filled) and mean fertilized eggs per recruit (open) are shown for a population with one large mating group when L_f=30 and r=1. The same basic patterns are predicted for multiple mating sites. Each line represents the same range of fishing mortalities, and each point represents fishing mortality increasing from 0 to 3 in increments of 1/3 moving from the right to the left. For the fourth rule (expected reproductive success), the two lines (eggs produced per recruit and eggs fertilized per recruit) overlap.

whereas sex change based on relative size or the relative frequency of individuals in a mating site is predicted to have similar dynamics to those for the fixed pattern of sex change. Thus, it is not possible to say that sex-changing stocks tend to be more or less resilient to fishing than are dioecious populations. However, the sex change rule clearly affects the predicted relationship between fishing mortality and the response of the stock to fishing.

Discussion

We apply a general approach using individual-based simulation models to determine the predicted effect of the pattern of sex change on the stock dynamics of a protogynous species. Although the model structure and parameter values considered will not apply to all commercially important protogynous species, it is important to realize that all the scenarios considered are identical except for the pattern of sex change. As a result, any predicted differences that arise between these situations are a result of the sex-change rule and indicate

that knowing simply that a species exhibits sex change but not what the behavioral rule of sex change is will lead to an incomplete ability to understand and predict the dynamics of the stock and its response to fishing or management strategies.

Independent of the sex-change rule, the protogynous stocks are always predicted to be sensitive to the size-selective fishing pattern. Mean population size is always predicted to decrease as fishing mortality increases, despite the fact that we have assumed that recruitment is strongly density dependent and that the species is very productive. Stocks are predicted to crash even at low fishing mortality when the size-selective fishing pattern targets all reproductive size classes and for the fixed sex change rule whenever all male sizes sizes are targeted by the fishery. It will be necessary but not sufficient to avoid overfishing at spawning aggregations. Our results indicate that it will also be important to allow smaller and nonreproductive individuals to escape fishing as well. These results indicate that independent of the exact pattern of sex change, management strategies for all protogynous stocks need to be sensitive to the size-selectivity of

the fishing pattern in relation to size at maturity and size at sex change observed in the population, and a failure to do so can lead to a sudden and unexpected collapse of the fishery—a collapse from which it may be difficult to recover.

We assume in all cases that the same cues determine both the probability of maturity and the probability of sex change within a species. For example, when sex change was affected by the relative size of individuals at the mating site, we assume that this same cue affected the probability of maturing. This assumption has a large effect on the predicted dynamics of the stock. Alternatives exist. For example, the size at which fish mature could be determined by endogenous rather than exogenous factors even in a population where the probability of sex change is affected by external cues. If this were the case, the population can easily be fished into a situation where it cannot compensate for size-selective fishing and is predicted to crash for any fishing pattern that targets reproductive individuals. For example, when $L_f=30$ and $r=1$, populations with plastic size at maturity and sex change were not predicted to crash independent of fishing mortality. In contrast, simulations where populations were assumed to have fixed size at maturity rules ($L_m=20$) but plastic patterns of sex change crashed at most fishing mortalities with $L_f=30$ and $r=1$. Hence, knowledge of the cues determining both maturity and sex change will be important in predicting and understanding larval production and the effect of fishing on a population.

It is possible to argue that a protogynous species with fixed patterns of sex change may have very different dynamics than dioecious stocks, but the compensatory patterns of sex change will be less sensitive to fishing and exhibit dynamics very similar to their dioecious counterparts. However, our results indicate that even stocks with plastic patterns of sex change are predicted to have dynamics distinctly different from otherwise identical dioecious populations. For example, sperm limitation is predicted to occur for all sex change rules, except for the pattern where sex change is determined by expected reproductive success (rule 4). However, even a stock exhibiting the reproductive sucess rule has dynamics that are distinctly different from those of a dioecious species because a change in the size distribution of the population due to size-selective fishing is predicted to have a large effect on the productivity and sex ratio of the protogynous population. Similarly, mating group size is predicted to affect the stock dynamics in all cases except for the reproductive success rule. Therefore, although knowing the pattern of sex change is predicted to be important in understanding stock dynamics, it is also clear that the pattern of sex change must be considered in the context of the mating system of the stock, as well as in the context of the basic biology of the stock.

Protogynous stocks are thus predicted to be sensitive to the fishing pattern, and nonlinear stock dynamics are possible when fishing operations target a wide range of fish sizes. However, each stock is also predicted to have a unique response to the same fishing pattern (Figs. 4–6) and to have different relationships between traditional spawning-per-recruit measures and changes in mean population size with fishing mortality (Figs. 1, 2, and 7). As a result, monitoring changes in spawning stock biomass per recruit or egg production per recruit alone will not make it possible to determine the relationship between these measures and mean population size or to know whether the population is at risk for large and sudden declines in population size. Our results indicate that although it is important to know whether sex change occurs when managing a stock, it will also be important to know what endogenous or exogenous cues induce sex change and how behavioral patterns and life history strategies affect the demographic rates of the stock.

Plasticity is not predicted to yield populations that have stock dynamics that are identical to those of dioecious species, and the performance of spawning-per-recruit measures and the relationship between egg production and population size differed greatly between all four patterns of sex change, despite the fact that the basic patterns of growth, survival, and fecundity where identical between all the scenarios considered. Because sperm limitation is more common with the fixed and relative size rules of sex change, these situations are predicted to have the greatest difference between classic SPR measures and the production of fertilized eggs. Clearly it is not just whether a population changes sex or not, but also how sex change is induced, that determines the population's predicted response to fishing and the performance of spawning-per-recruit measures in predicting and indicating the effect of fishing on the population.

Although it is important to know what life history strategy and behavioral patterns are observed in a species, these alone will not always be sufficient to predict expected changes in population size and productivity under new conditions. Instead, knowledge of the plasticity of behavioral and life history patterns, as well as information about the internal and external cues that induce phenotypic changes, may also be necessary. Phenotypic plasticity is often expressed as a threshold response (such as sex change) to a continuous endogenous or exogenous cue. Therefore, as predicted by our model, plasticity can generate nonlinear changes in important demographic characters. An understanding of the natural variation in behavior and life history combined with knowledge of fish vital rates and environmental conditions will lead to a better understanding of and ability to predict the response of a stock to fishing mortality, environmental changes, and specific management strategies.

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