

Abstract—Fisheries models have traditionally focused on patterns of growth, fecundity, and survival of fish. However, reproductive rates are the outcome of a variety of interconnected factors such as life-history strategies, mating patterns, population sex ratio, social interactions, and individual fecundity and fertility. Behaviorally appropriate models are necessary to understand stock dynamics and predict the success of management strategies. Protogynous sex-changing fish present a challenge for management because size-selective fisheries can drastically reduce reproductive rates. We present a general framework using an individual-based simulation model to determine the effect of life-history pattern, sperm production, mating system, and management strategy on stock dynamics. We apply this general approach to the specific question of how size-selective fisheries that remove mainly males will impact the stock dynamics of a protogynous population with fixed sex change compared to an otherwise identical dioecious population. In this dioecious population, we kept all aspects of the stock constant except for the pattern of sex determination (i.e. whether the species changes sex or is dioecious). Protogynous stocks with fixed sex change are predicted to be very sensitive to the size-selective fishing pattern. If all male size classes are fished, protogynous populations are predicted to crash even at relatively low fishing mortality. When some male size classes escape fishing, we predict that the mean population size of sex-changing stocks will decrease proportionally less than the mean population size of dioecious species experiencing the same fishing mortality. For protogynous species, spawning-per-recruit measures that ignore fertilization rates are not good indicators of the impact of fishing on the population. Decreased mating aggregation size is predicted to lead to an increased effect of sperm limitation at constant fishing mortality and effort. Marine protected areas have the potential to mitigate some effects of fishing on sperm limitation in sex-changing populations.

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The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish

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Fisheries models are generally used to predict the impact of fishing on stock dynamics and yield (Quinn and Deriso, 1999; Haddon, 2001). Classic models have focused mainly on growth, fecundity, and survival of species, without considering the impact of mating patterns on reproduction, survival, and recruitment. It is now recognized that life-history strategies and mating behavior will affect stock dynamics. Even so, general quantitative predictions regarding the effect of specific life-history patterns on fished populations are limited and further theory is needed (Levin and Grimes, 2002). It is likely that management strategies taking into account a species' reproductive behavior will greatly improve our ability to manage stocks (e.g. Beets and Friedlander, 1999). We would also like to know when the mating behavior and reproductive strategies of a stock will be worth investigating and when traditional management techniques will be sufficient. For example, in a management context, how do sex-changing stocks differ from separate-sex species? Here, we take an initial step toward generating a theory of the combined effect of life history and mating patterns on stock dynamics by focusing on the potential for and effect of sperm limitation in a protogynous (female to male) sex-changing stock. We focus on protogyny for this article because

numerous protogynous species are commercially important, namely red porgy (*Pagrus pagrus*), gag grouper (*Myceteroperca microlepis*), and California sheephead (*Semicossyphus pulcher*).

Sex-changing fish present a unique challenge for management because size-selective fisheries have the potential to drastically reduce reproductive rates and population size at levels of fishing that would not pose a problem for dioecious (separate-sex) species (Huntsman and Schaaf, 1994; Armsworth, 2001; Fu et al., 2001). On the other hand, protogynous stocks may be less sensitive to the removal of large individuals if females are not fished and fertilization rates remain high. Many commercially important species are known to change sex (Bannerot et al., 1987; Shapiro, 1987; Coleman et al., 1996; Brule et al., 1999; Adams et al., 2000; Armsworth, 2001; Fu et al., 2001). Previous models have shown that sex-changing fish may be vulnerable to fishing (Bannerot et al., 1987; Huntsman and Schaaf, 1994; Armsworth, 2001; Fu et al., 2001).

Complications arise because the effect of fishing on a sex-changing species is mediated by many aspects of their reproductive biology, such as sex ratio, size-dependent fecundity, spawning aggregation size, and reproductive skew. Furthermore, patterns of sex change have cascading effects on the sex ratio, social interactions, population

fecundity, and male sperm production—all of which can affect stock dynamics. Thus, we cannot treat sex change as an isolated aspect of a species. Instead, we must consider sex change within the context of the mating system and the life history of the species to make general predictions. Behaviorally appropriate models are required to generate constructive qualitative and quantitative theory. Past theory has indicated that sex-changing populations exhibit stock dynamics that often differ from those of dioecious populations (Bannerot et al., 1987; Huntsman and Schaaf, 1994; Armsworth, 2001; Fu et al., 2001). Furthermore, protogynous stocks are predicted to be sensitive to fishing pattern and may exhibit nonlinear dynamics that could lead to population crashes (Armsworth, 2001). However, it is not known which aspects of the mating behavior and life history pattern of sex-changing stocks drive these differences. Here we focus on comparing a protogynous stock with an otherwise identical dioecious population to determine the effect of mating aggregation size, fertilization rates, and life history pattern on stock dynamics.

Size-selective (or age-selective) fisheries can impact a species through a decrease in spawning stock biomass, in general and through the removal of highly fecund larger and older individuals, in particular (Sadovy, 2001). However, in protogynous species, fisheries that preferentially remove large males can also change the population sex ratio; however, the exact effect of fishing pressure on stock dynamics in a protogynous species is complex. At one extreme, the complete removal of males from the population would cause a stock to crash, potentially making sex-changing species more vulnerable than dioecious species in the face of high fishing pressures. At the other extreme, sex-changing species may be less affected by size-selective fisheries if female fecundity limits recruitment and males are not removed in such numbers as to reduce mating or fertilization rates. Currently, there is no theory that predicts the potential for sperm limitation in protogynous stocks as a function of gamete production, fertilization rates, and mating pattern.

It has been suggested that marine reserves may be a viable management option for species where highly fecund older individuals are critical to reproduction (Levin and Grimes, 2002). However, no theory exists that can predict the impact of marine reserves on stock dynamics in sex-changing species. We consider the impact of a no-take marine reserve on the stock dynamics. We compare the effect of setting aside 0–30% of the spawning population in a reserve. We assume that larval production is exported from within the reserve to the rest of the population and determine whether the reserve can mediate some of the effects of fishing outside the reserve because this represents the optimal scenario for marine reserves. We also compare mean catch rates in the presence and absence of a reserve as a function of fishing mortality.

Spawning-per-recruit (SPR) measures are often used to estimate the impact of fishing on a stock (Parkes, 2000; Jennings et al., 2001). Ideally, a spawning-per-recruit measure would keep track of per-recruit production of larvae or eggs (Jennings et al., 2001). However, spawning stock biomass per recruit (SSBR) is commonly used to estimate

the reproductive output per recruit at different intensities of fishing. One assumes that the biomass of mature fish is linearly related to reproductive output, which may be the case when egg production limits biomass and fecundity increases linearly with biomass. In protogynous stocks, overfishing of males alone may decrease fertilization rates and hence reproductive output without affecting either female biomass or egg production. Thus, in protogynous stocks or sex-selective fisheries, classic measures of spawning per recruit may misrepresent the impact of fishing on the stock's reproduction and hence population stability (Punt et al., 1993). We examine a variety of per-recruit measures and determine their ability to predict changes due to exploitation in mean population size.

In this study, we describe a general approach using sex- and size-dependent individual-based simulation models that predict reproduction, size distribution, and sex ratio in fished populations as a function of mating system and sex-change pattern. We examine the case where sex change occurs at a specific size threshold. We recognize that plastic and socially mediated sex-change patterns have been observed, and our results will apply only to species with fixed sex change. We explore the impact of mating aggregation size, sperm production, and asymptotic fertilization rates on the predicted stock dynamics in the presence of exploitation. We make predictions regarding the effects of fishing on population size, reproduction, sex ratio, size distribution, and fertilization rates. We also compare our results to previous work and discuss future directions.

Methods

We used an individual-based simulation to predict the size distribution, individual and population fecundity, population sex ratio, fertilization rate, and population size as a function of fishing mortality (Fig. 1). Individuals vary in age, size, sex, and mating site. Population size varies as a function of baseline survival, fishing mortality, reproduction, and larval recruitment. Reproduction depends on the pattern of sex change, mating system, sex ratio, mating site, and fecundity (or fertility) of individual males and females. For each annual time period, we determined individual survival, the size and age of these individuals in the next time period, and the total production of surviving offspring by those individuals. Initial analyses showed that a stationary size, sex, and age distribution is found within approximately 50 time periods and is independent of the initial population conditions. Thus, we simulated 100 time periods prior to examining the impact of fishing on stock dynamics to ensure that the population had already reached the stationary size and sex distribution for that scenario and set of parameters. We then examined the model for 100 reproductive seasons in the presence of fishing with a constant mean fishing mortality. Because a number of elements of the model were stochastic, we examined 20 simulations for each scenario and set of parameter values. Initial analyses indicated that 20 simulations were more than sufficient to lead to low variability in the key measures of interest. We assumed that reproduction occurs at the level of the mating

group at different reproductive sites. Individual survival, maturation, sex change, and mating site were determined stochastically as described below.

Fishing and adult survival

We assumed that adult survival is density independent but depends on fishing selectivity, fishing mortality, and baseline adult mortality in the absence of fishing. For simplicity, we assumed that age and size do not affect nonfishing adult mortality μ_A . We assumed that the fishery is size selective; we let L represent fish size, F represent annual fishing mortality, L_r represent the size at which there is 50% chance an individual of that size will be taken, and r represent the steepness of the selectivity pattern. Then fishing selectivity per size class $s(L)$ is given by

$$s(L) = \frac{1}{1 + \exp(-r(L - L_r))} \quad (1)$$

and adult annual survival becomes

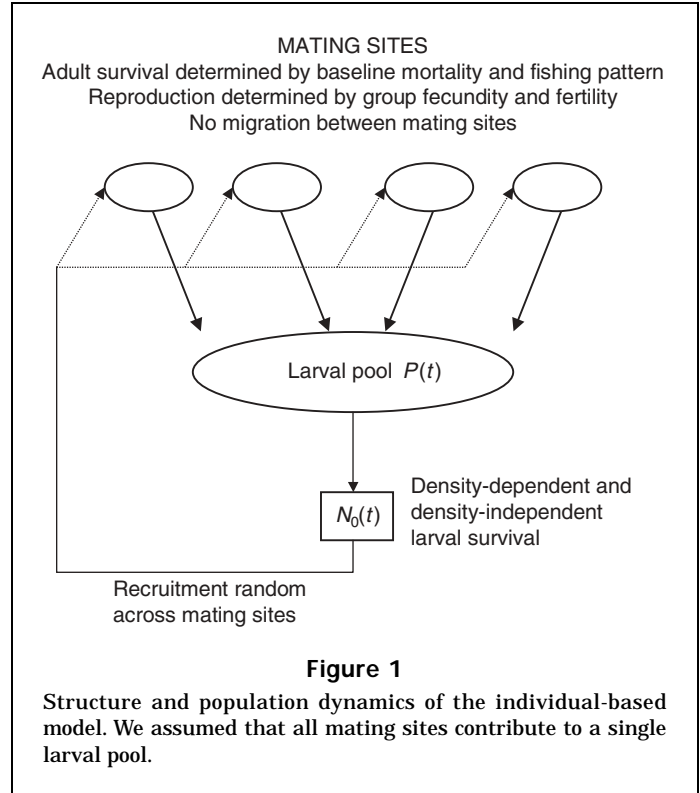
$$\sigma(L) = \exp(-\mu_A - Fs(L)). \quad (2)$$

We assumed that fishing does not differentially affect the sexes independent of size. We recognize, however, that for some species this may not be the case. We also assumed that fishing occurs each year prior to reproduction and can represent either pulse or continuous fishing with an annual mortality F . We let $N_a(t)$ represent the number of individuals in age class a at time t so that population size $N(t) = \sum_a N_a(t)$.

Population dynamics

We assumed that the number of larvae that enter the population is determined by the production of fertilized eggs $P(t)$ and the probability that those larvae will survive to recruit. $P(t)$ is determined by the adult fecundity and fertilization rates described below. For computational tractability, we also assumed that a population ceiling N_{\max} exists (Mangel and Tier, 1993, 1994). However, we chose N_{\max} large enough that the stable population size was below the ceiling. Larval survival has both density-independent and density-dependent components (e.g. Cowen et al., 2000; Sale, 2002). We used a Beverton-Holt recruitment function to determine larval survival to the next age class (Quinn and Deriso, 1999; Jennings et al., 2001). Larvae represented the zero-age class $N_0(t)$ and thus the number of larvae surviving to recruit in any year t is given by

$$N_0(t) = \begin{cases} (\alpha P(t)) / (1 + \beta P(t)) & \text{if } (\alpha P(t)) / (1 + \beta P(t)) \\ & + \sum_{a=1} N_a(t) \leq N_{\max} \\ 0, N_{\max} - \sum_{a=1} N_a(t) & \text{if } (\alpha P(t)) / (1 + \beta P(t)) \\ & + \sum_{a=1} N_a(t) > N_{\max}, \end{cases} \quad (3)$$



where α gives density-independent survival; and β determines the strength of the density-dependence in the larval phase. In this function, we used the number of fertilized eggs produced, $P(t)$, rather than spawning stock size. We selected parameter values for larval survival that allowed the mean population size to be stationary near the ceiling in the absence of fishing. We assumed a single larval pool and that larvae recruit to mating sites at random (Fig. 1). The population was open between mating sites and we were simulating the entire stock. Thus, there was no emigration to or immigration from outside populations.

Growth dynamics

We assumed that all larvae enter the population at the same size, L_0 . We assumed that growth is deterministic and independent of sex or reproductive status. We used a discrete time version of the von Bertalanffy growth equation (Beverton, 1987, 1992) to determine growth between age classes of surviving adults in which 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 $L(t+1)$ as follows:

$$L(t+1) = L_{\text{inf}}(1 + \exp(-k)) + L(t)\exp(-k). \quad (4)$$

Mating system

We assumed that reproduction occurs at the level of the mating group, and we examined the effect of varying mating group size and the number of mating sites. We assumed

that juveniles and adults exhibit site fidelity but that larvae settle randomly among mating sites. We also assumed that the population carrying capacity is split equally among the mating sites and that 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. Therefore, mating sites do not limit recruitment but may affect reproductive rates. We examined three cases: 1) the entire population mates at one site (one 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). For simplicity, we assumed that within a mating site, individuals mate in proportion to their fertility and fecundity. Therefore, large males and females have higher expected reproductive success. However, we assumed that all males that are large enough to change sex have a chance of reproducing proportional to their fertility. This is equivalent to assuming that females exhibit a mate choice threshold (Janetos, 1980) that has evolved with the size-at-sex change and that females have an equal probability of mating with males above this size threshold. However, a large male mating advantage clearly still exists. We also assumed that fishing mortality remains constant as mating aggregation size varies. Thus, we assumed that fishing effort per site does not increase as the number of mating sites decreases. An alternative would be to assume that total fishing mortality increases as the number of mating aggregations decreases.

Maturity

The probability that an individual matures $p_m(L)$ is determined by size. Once an individual matures, she remains female until sex change (see below). We let L_m represent the length at which 50% of the individuals will have matured.

$$p_m(L) = \frac{1}{1 + \exp(-q(L - L_m))}, \quad (5)$$

where q determines the steepness of the probability function.

Sex change

The probability of sex change, $p_c(L)$, is a logistic function of absolute size L

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

where L_c represents the size at which 50% of the individuals will change sex from female to male and ρ is a constant.

Reproduction

We assumed that female fecundity $E(L)$ depends on individual size according to the allometric relationship

$$E(L) = aL^b, \quad (7)$$

where a and b are constants.

Once an individual has changed sex (as determined by the sex change rule described above) sperm production (in millions) $S(L)$ is given by

$$S(L) = cL^d, \quad (8)$$

where c and d are constants.

Size-dependent fecundity has been measured in many fish species (e.g. Gunderson, 1997). A general allometric relationship between sperm production and size has not been established. Therefore, we assumed that male gamete production increases with size at the same rate as that for females ($b=d$). We also assumed that males produce many more sperm at any body length than females produce eggs. Clearly, other possible patterns exist. We examined the case where males produce from 10^2 to 10^6 sperm for every egg produced by a female. In the pelagic spawning wrasse (*Thalassoma bifasciatum*), large males release approximately 1000 times more sperm than females release eggs (Schultz and Warner, 1991; Warner et al., 1995).

We used recently published data on sperm production and fertilization rates in the bluehead wrasse (*Thalassoma bifasciatum*) to generate a biologically appropriate fertilization function for our model (Warner et al., 1995; Petersen et al., 2001). It is critical to consider a biologically appropriate form for the function to express fertilization rates when considering the potential for sperm limitation. The probability an egg will be fertilized is an increasing function of the number of sperm available for that mating (Fig. 2). The number of eggs released per mating also affects the fertilization rate (Fig. 2). For simplicity, we calculated the average expected fertilization rate per mating site based on the total production of sperm and eggs at the site. We let S represent the number of sperm released (in millions) and E the number of eggs released at each mating site. We assumed that the proportion of eggs fertilized per mating site p_F is given by

$$p_F = \frac{S}{1 + (\kappa E + \chi)S}, \quad (9)$$

where κ and χ are constants fitted to the data.

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.

Measures of spawning stock biomass per recruit

To measure the impact of fishing on stock dynamics, we computed the total spawning stock biomass per recruit starting from the beginning of fishing for the next 50 years. We used 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 calculated total female and male spawning stock biomass

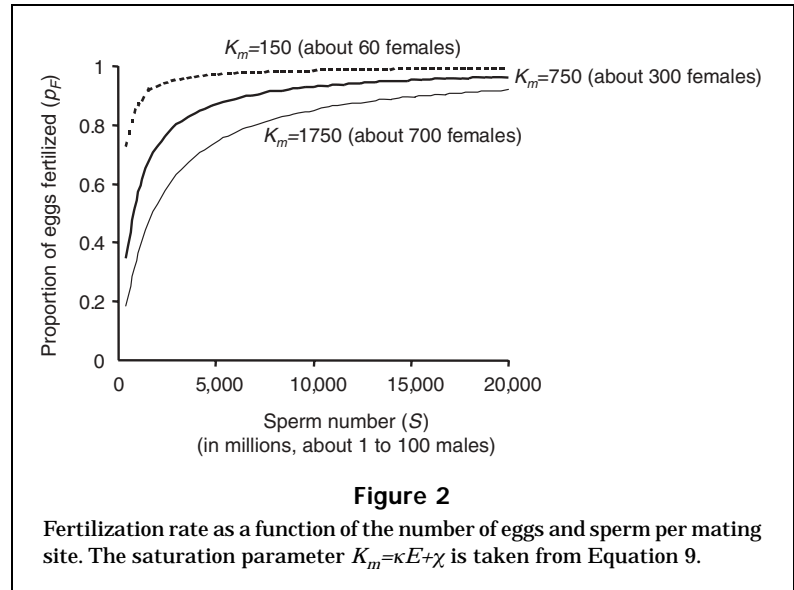
per recruit (SSBR). We also kept track of the total fecundity (egg production per recruit), fertility (sperm production per recruit), and eggs fertilized per recruit.

Marine reserves

We examined the effect of no-take marine reserves on the predicted stock dynamics by comparing the stock dynamics in the presence and absence of reserves. Without a reserve, individuals at all mating sites are subject to fishing. In the presence of a no-take marine reserve, we “protect” a percentage of the mating sites (and thus the population) from fishing. We examined cases in which 0%, 10%, 20%, and 30% of mating sites were protected from fishing. We assumed that the population is completely open among mating sites. Thus, eggs produced from all mating sites enter one larval pool and recruitment occurs randomly between mating sites. Clearly other possibilities exist and could be considered in future analyses, but this case represents a reasonable baseline situation to consider because many marine fish have pelagic larval phases. We also recognize that these analyses ignore the effect of interactions between species within the reserve on stock dynamics. We examined two situations. In the first case, reduced fishing effort occurs when mean fishing mortality is decreased in the presence of reserves because fishing mortality (F) at the unprotected sites remains the same as before the reserve. In the second case, the redistribution of fishing effort occurs when mean fishing mortality across all sites remains the same because fishing mortality increases at the unprotected sites.

Comparison of sex-changing stocks and dioecious stocks

Ideally, we would like to distinguish the effects of sex change in isolation from the confounding effects of mating pattern, sex ratio, survival, growth, and population fecundity on stock dynamics. To differentiate whether sex change in isolation or other aspects of the mating system determine the predicted stock dynamics, we also examined a version of the model described above for a population where sex is fixed at birth. In this dioecious population, we keep all aspects of the stock constant except for the pattern of sex determination (whether the species changes sex or is dioecious). One would generally expect a dioecious population with no differences between the sexes in mortality to exhibit a 50:50 sex ratio (Fisher, 1930; Trivers, 1972; Charnov, 1982). However, we wanted to control for all differences between the dioecious and protogynous stocks other than the sex-determination pattern. Therefore, we considered the same sex ratio at maturity (0.67=the proportion of adults that are female) as found in the sex-changing population in the absence of fishing. Assuming no sex-specific differences in survival to maturity, this is the same as assuming a 0.67 sex ratio at birth. In this model, individuals remain one sex (determined randomly at birth) throughout their lifetime.



Fishing is size but not sex selective. We assumed that males mature at the same size as females.

Parameter values

We used previous research 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. Because nothing is known about fertilization rates in the California sheephead, we generated κ and χ (Eq. 9) by fitting a line through the estimated values of K_m for small and large bluehead wrasse females as a function of their mean egg production (see Table 1 and Fig. 2; Warner et al., 1995; Petersen et al., 2001). For parameter values and sensitivity analyses see Table 1.

Results

We present the average across 20 simulations of the mean population measures of the last 50 years for each simulation. The variation around the mean in all measures considered was very low (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 had died before the end of the simulation. When the ratio of sperm to eggs is 10^4 to 10^6 , a single male can fertilize all of the eggs in the population. When the ratio of sperm to eggs is 10^2 , sperm limitation occurs even in the absence of fishing. Therefore, we present results for the case where the ratio of sperm to eggs is 10^3

Table 1
The following parameters were used in the model.

Parameter	Baseline 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 fecundity relationship (Warner, 1975)
c	$10^{-3}a$ ($10^{-2}a$, $10^{-4}a$)	constant in the sperm production function (measured in millions of sperm)
d	b	exponent in the fertility relationship (Warner, 1975)
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
Maturity		
L_m	20 cm	length at which 50% of fish mature (Warner, 1975; Cowen, 1990)
q	1	shape parameter in the maturity function
Sex change		
L_c	30 cm	length at which 50% of fish change sex (Warner, 1975; Cowen, 1990)
ρ	1	shape parameter in the sex change function

and fertilization rates are 100% in the absence of fishing, but the population must have multiple males for high fertilization rates. For all the results presented in our study we assumed a fixed sex-change pattern, mating among males and females at each site proportional to gamete production, and larval export among mating sites. We also assumed, unless otherwise noted, a sharp size-selective fishing pattern ($r=1$) and that the probability of sex change and removal of sex-changing fish by the fishery are centered at the same mean size or $L_f=L_c$. Clearly, the results presented in our study may not apply to cases where these assumptions are not met.

General patterns predicted by the model

First, we examined the general effect of fishing mortality on the sex-changing stock for the case when one mating site exists. When $L_f=L_c$, eggs produced per recruit decrease only slightly with fishing mortality (e.g. a 3% drop as fish-

ing mortality increased from 0 to 3, Fig. 3A). However, the mean number of eggs fertilized (both total and per recruit) decreases sharply as fishing mortality increases (e.g. a 30% drop as fishing mortality increased from 0 to 3, Fig. 3A). The number of recruits per year decreases as well. As fishing mortality increases, male spawning stock biomass per recruit decreases dramatically, whereas changes in female spawning stock biomass would be practically undetectable (90% drop for male SSBR, compared with a 3% drop for female SSBR as F increases from 0 to 3, Fig. 3B). Because of the drop in male SSBR, total spawning stock biomass (males and females) per recruit also decreases as fishing mortality increases. Sperm production per recruit is predicted to decrease with increasing fishing mortality (Fig. 3C).

Sensitivity of stock dynamics to fishing pattern

In general, mean population size decreases as fishing pressure increases (Fig. 4A). The adult sex ratio (measured as

the percentage of mature individuals that are female) also increases as fishing mortality increases (Fig. 4B) and the mean size of adults in the population decreases. These patterns depend on fishing being size selective, which causes a disproportional take of males. If the size-selectivity of the fishery targeted smaller size classes ($L_f < L_c$), a decline in annual biomass removed by the fishery is predicted with increasing F and the stock is predicted to crash at a relatively low fishing mortality (Fig. 4C). If the fishery is less selective ($r=0.1$, $L_f=L_c$), the population is also predicted to crash for most fishing mortalities. Thus, allowing some proportion of mature males to consistently escape fishing is critical even at low fishing mortality. As fishing mortality increases, the predicted biomass removed by the fishery increases with diminishing returns (Fig. 4C). When $L_f=L_c$ the biomass removed by the fishery does not continue to increase with F because all males above the size at sex change are being removed by the fishery. In this case, the males in the population are essentially breeding only once before they are taken by the fishery. For the range of fishing mortality considered, we did not observe a decline in biomass taken with increasing F unless $L_f < L_c$ or $r=0.1$. If more size classes are allowed to escape fishing ($L_f > L_c$), the general patterns remain the same, but for the same fishing mortality (F), the effect of fishing on the population is less (Fig. 4). Female biomass does not decrease much with fishing mortality when $L_f=L_c$ even though some females are removed by the fishery because the probability of a female changing sex is the probability of it being fished. Therefore, female loss due to the fishery affects male biomass rather than female biomass in the population.

Sperm limitation and production

The removal of large males from the population is predicted to cause sperm limitation and decreased fertilization rates (Fig. 3, A and C), leading to a decrease in mean population size (Fig. 4A). The degree to which the fertilization rate and thus the population size decreases depends to a great extent on the pattern of sperm production and fertilization. We assumed that only a few males are needed to fertilize the eggs of many females (Fig. 2). We also assumed that per-capita reproduction and recruitment are high even at a low population size (Barrowman and Myers, 2000). Thus, protogynous populations with lower sperm production or fertilization rates would experience greater effects from fishing than predicted in the present study. Similarly, populations with lower production or survival would experience larger decreases in population size even with the same level of sperm limitation and fishing. In general, however, the removal of males alone from a protogynous population with a fixed sex change is predicted to cause decreased fertilization rates and lower mean population size even when the fertilization rate function is asymptotic and individual male sperm production is high.

Mating aggregation size

As mating aggregation size decreased and fishing mortality and effort remained constant, the effect of fishing on the pop-

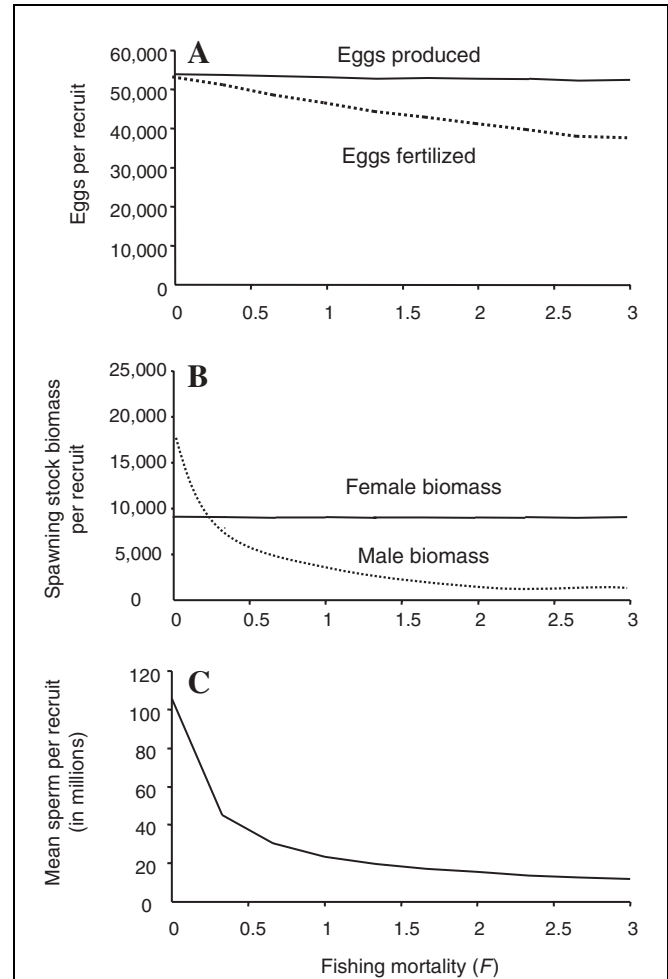


Figure 3

Spawning-per-recruit measures. Results are presented for the sex-changing stock with one mating site when $L_f = L_c$ and $r=1$. Means across 20 simulations are given. For details see the general text.

ulation increased. As described above, we assumed that fishing effort would not be concentrated on the few large mating aggregations and thus increase total fishing mortality. The sex ratio, mean size, mean fecundity, and mean fertility all remained the same across different mating aggregation sizes with constant fishing mortality. However, the mean fertilization rate and number of fertilized eggs per recruit decreased with mating group size (Fig. 5) even though male biomass and SSB remained the same. Both predicted mean population size and biomass taken decreased as fishing mortality increased (Fig. 5). This pattern was generated by sperm limitation in small mating groups. Smaller groups have higher probabilities that sperm production within the group will not be sufficient to fertilize the eggs produced within the mating group. Small mating aggregations may not only be sperm limited but also be male limited and fail to reproduce completely; populations with small group sizes (50 individuals or less) were predicted to become extinct in

5–25% of the simulations as fishing mortality (F) increased from 0 to 1. The impact of mating group size on stock dynamics is thus predicted to be nonlinear. A threshold mating aggregation size appeared to exist below which sperm limitation and reproductive failure become common.

Spawning-per-recruit measures

For size-selective fishing, the spawning stock biomass per recruit of females is not predicted to decrease significantly with increased fishing mortality as long as some male size classes escape fishing ($L_f \geq L_c$). However, male biomass per recruit and sperm production per recruit are both predicted to decrease. Although egg production is not predicted to

decrease with increasing size-selective fishing pressure, the number of fertilized eggs is predicted to decrease. When all male size classes are fished ($L_f < L_c$), the stock is predicted to crash and therefore clearly female biomass and egg production are predicted to decrease with fishing mortality. In general, the predicted decrease in mean population size and reproduction is driven for the most part by decreased sperm production and consequently a reduction in the number of eggs fertilized per recruit. The relationships between fishing pressure and the classic spawning-per-recruit measures do not indicate the true effect that fishing is predicted to have on the protogynous population (Fig. 6). When $L_f \geq L_c$ female spawning stock biomass per recruit and eggs produced per recruit showed almost no effect of fishing on the population, even as mean population size decreased. Because of the size-selective fishing pattern, total and male biomass per recruit decreased with fishing mortality and decreasing mean population size. However, male and total biomass per recruit did not reflect the increased effect of fishing on populations with smaller mating aggregations. The production of fertilized eggs per recruit decreased with increased fishing pressure and decreased more sharply for smaller mating aggregations. Only the number of fertilized eggs per recruit could assess the predicted effect of fishing on the protogynous population. Thus, classic SPR measures were predicted to fail in the presence of sperm limitation to assess the impact of fishing on a protogynous stock.

Marine reserves and fishery management

In the situation considered in this study, the pattern of fishing is more important to stock dynamics than the presence of marine reserves. We assumed a size-selectivity that allowed on average 50% of individuals of sex-changing size to escape the fishing gear. Thus, although the sex ratio does increase (become more female) by 20–40%, all males are not lost from the population (when $L_f \geq L_c$ and $r=1$). If fishing selectivity occurs at a smaller size, then the effects on the population are predicted to be much greater and the protogynous stock would suddenly become more affected than the dioecious population. For example, at $L_f=25$ cm the protogynous stock is predicted to crash whenever $F \geq 1$. This occurs not because of a reduction in the production of eggs but rather because of a failure to fertilize the eggs produced by surviving females. When males of all size classes are fished, populations can become male limited and fertilization rates drop drastically. A decrease in the production of fertilized eggs can lead to a decrease in female biomass, but it is the removal of males rather than females that causes this decline.

When fishing effort is not redistributed after the formation of a reserve, the impact of fishing on the mean population size and SPR measures is predicted to decrease (e.g. Fig. 7A). However, if fishing effort is redistributed among unprotected areas, the benefit of the reserves to the protogynous stock decreases (Fig. 8A). Protecting some sites allows large males to

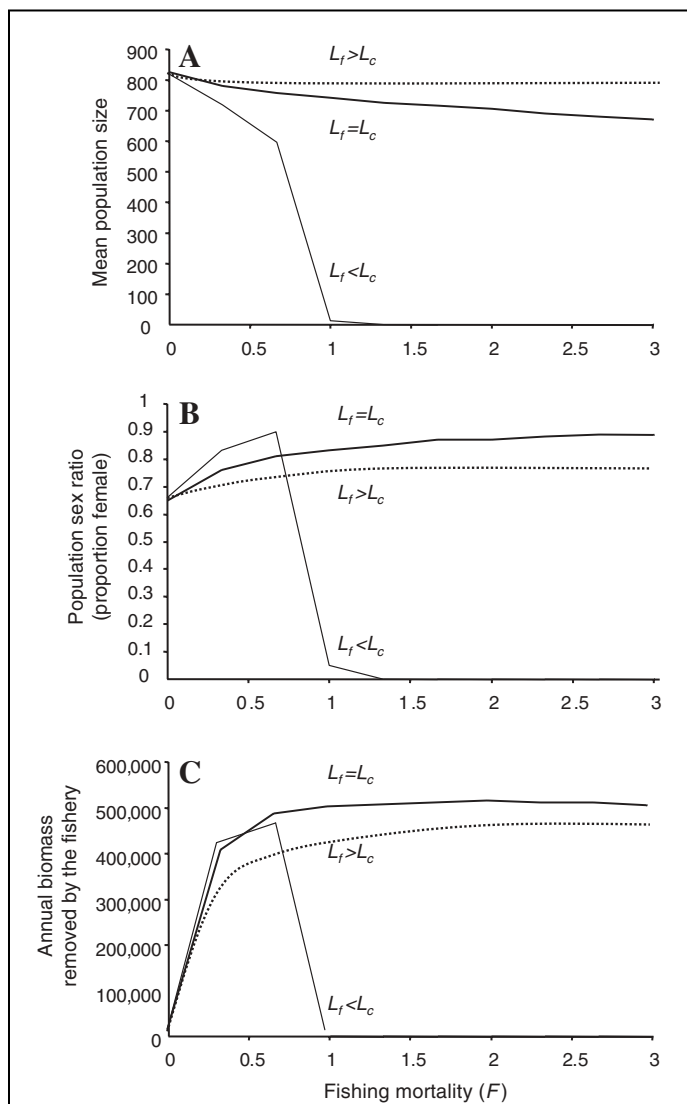


Figure 4

The effect of size-selective fishing on stock dynamics. We present results for the sex-changing stock with one mating site when $r=1$. Means across 20 simulations are given. For details see the general text.

escape fishing and thus increases the production of fertilized eggs at the population level. However, yield decreased proportionally to the percentage of sites protected by the reserve unless fishing effort is redistributed among the remaining sites. We assumed that fish do not move between sites after the larval stage, and thus larger and older individuals do not leave the reserve and become exposed to fishing. Although this assumption is clearly appropriate for some species, it is important to realize that the dynamics and predictions would differ for more closed populations or migratory species. For the fishing pattern and biological scenario examined in this study, marine reserves are not predicted to increase biomass available to the fishery (Figs. 7B and 8B).

Dynamics of dioecious versus protogynous stocks

In the dioecious stock with a single randomly mating aggregation, both male and female biomass per recruit and fecundity or fertility per recruit are predicted to decrease as fishing mortality increases (Fig. 6). Because both egg production and sperm production decrease with increased fishing pressure in the dioecious stock, the number of eggs fertilized per recruit did not differ much from the other SPR measures. Thus, SSBR and eggs per recruit also indicated the impact of fishing on the stock in dioecious stocks with large mating aggregations. The percent drop in population size and fertilized egg production is predicted to be much greater in dioecious species and occurred more quickly than in the sex-changing stock because of a reduction in overall population fecundity even in the absence of decreased fertilization rates. However, dioecious stocks are predicted to exhibit larger mean population size for the same fishing mortality and to support a larger fishery because of the additional egg production of large fecund females. At very small mating aggregations, sperm limitation is predicted even in the dioecious stock and fertilized eggs per recruit become a better indicator of stock dynamics in the presence of fishing. Dioecious stocks are also predicted to benefit from marine no-take reserves through the protection of large fecund females (Fig. 7).

Discussion

In this study we developed a general framework that examines the consequences to

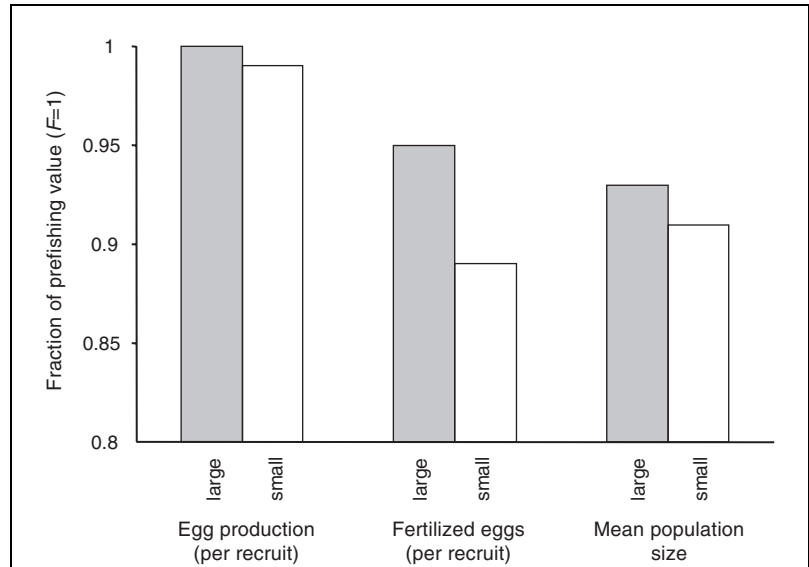


Figure 5

Mating aggregation size affects the response to fishing. Large (one large mating aggregation) and small (10 smaller mating aggregations) situations are compared. Percent change in the presence of fishing (from $F=0$ to $F=1$) in egg production per recruit, mean fertilized egg production per recruit, and mean population size are given. Total population fecundity and mean body size are lower for the smaller mating aggregations.

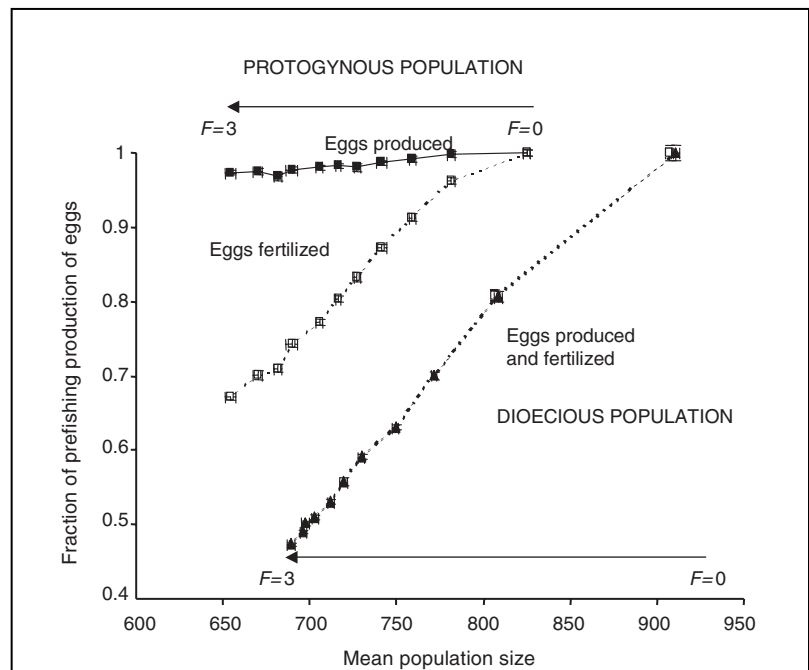


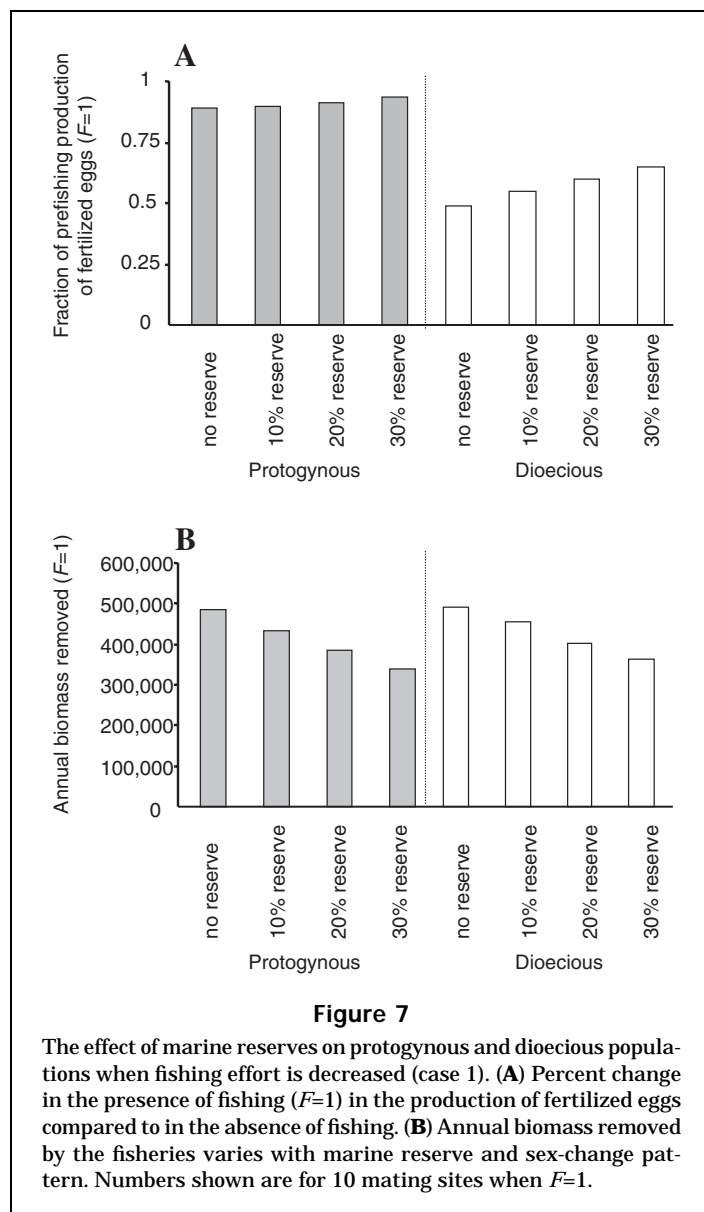
Figure 6

Spawning-per-recruit (SPR) measures in a protogynous (squares) and dioecious (triangles) stock: Mean egg production per recruit (filled) and mean fertilized eggs per recruit (open) are shown for a randomly mating population with one large mating group. Error bars indicate the standard error of the mean. For the dioecious population, the two SPR measures overlap.

fisheries management of a behaviorally and evolutionarily reasonable life-history and sex-change pattern. We based our assumptions and parameter values on patterns observed in natural populations that have presumably evolved given the life history tradeoffs and expected reproductive success associated with these behaviors. However, we made various assumptions that affect the predicted patterns such as a fixed sex-change pattern, male mating success proportional to sperm production, and a very resilient recruitment function. Despite these assumptions, a number of general patterns emerge.

Life-history pattern is important but not sufficient to predict stock dynamics

In general, we predicted that a protogynous stock with fixed sex change will respond to the same fishing pressure



differently than an otherwise identical dioecious stock. Understanding the life history of the population is clearly important to our understanding of stock dynamics. However, it is not possible to classify protogynous stocks simply as more or less sensitive to fishing. The differences between dioecious and sex-changing fish are relatively complex, and it is not the case that one life history is expected to be more or less vulnerable to fishing. Although the sex change and fishing pattern are important, they must be seen in the context of the mating system, reproductive behavior, and population dynamics of the species. If no male size classes escape fishing, then the sex-changing population will be much more sensitive to fishing and may crash even at low fishing mortality. When some male size classes escape fishing, an identical dioecious stock is predicted to experience a greater decrease in mean population size than the protogynous population. However, the protogynous species is predicted to be much more sensitive to mating aggregation size and sperm limitation. Protogynous stocks are predicted to benefit from marine protected areas at high levels of fishing mortality where sperm limitation is common at fished mating sites. In contrast, the dioecious stock is predicted to derive a greater benefit of marine reserves even at low fishing mortality because of the protection of large fecund females (Fig. 7). Although the sex-changing population is predicted to be less sensitive to fishing mortality overall, it is clearly very important to understand the exact details of the sex-change pattern and the size-selectivity of fishing in relation to sex change. It will also be important to understand the mating system and patterns of fertilization success and sperm production in males when managing a protogynous stock. Given the sensitivity of the sex-changing stock to the size-selective pattern of fishing, we recommend the precautionary approach of keeping fishing mortality sufficiently low so that some males of all size classes always escape fishing (Fig. 4C). Clearly, protogynous stocks cannot be managed as if they were dioecious.

Sperm limitation and mating aggregation size affect stock dynamics

The removal of large males from the population can cause sperm limitation, decreased fertilization rates, and decreased population size even in a resilient species with high sperm production. Sperm limitation will increase as mating group size decreases. In the present model, even small males produced relatively large amounts of sperm. If males are removed, populations with lower sperm production are predicted to be more sensitive to the removal of large fertile males. Our assumption of fertilization rates determined by total egg and sperm production per mating site will, if anything, have underestimated the potential for sperm limitation. Other mating systems and reproductive behaviors could lead to greater sperm limitation than predicted in our study. For example, species that have not evolved under sperm competition should be more affected by the removal of large males than

species with sperm competition because of decreased allocation to sperm production. Pair spawning among individuals could also lead to decreased fertilization rates. Reproductive behaviors often found in sex-changing species, such as territoriality, female choice, resource-defense polygyny, and mate monopolization, all lead to skewed reproductive success for males and could further decrease fertilization rates. Sperm limitation is predicted to occur, and an understanding of such factors as fertilization rate, sperm production, mating skew, and mating group size will increase our ability to understand and predict stock dynamics.

Traditional spawning-per-recruit measures can fail in the presence of sperm limitation

Although problems exist with traditional spawning-per-recruit measures in general (Parkes, 2000), they are especially problematic for sex-changing stocks. In the dioecious stock, the relationship between female and total spawning stock biomass per recruit exhibits a roughly linear relationship with population size. In the sex-changing stock, female fecundity does not reflect the changes in mean population size. Although total or male spawning stock biomass per recruit did decrease with decreased population size, the fit between these measures will depend greatly on the size-dependent sperm production of males, mating aggregation size, and other factors determining the potential for sperm limitation. Male or total spawning stock biomass per recruit alone cannot predict sperm limitation and thus will fail to predict the potential population crashes that may result. We conclude that any measure of spawning per recruit in a sex-changing species that does not consider sperm limitation and reduced fertilization rates has the potential to underestimate the impact of fishing on the population. The number of eggs produced or female spawning stock biomass can remain relatively unchanged in the face of high fishing mortality even as the population is predicted to decline. However, the failure of classic spawning-per-recruit measures in the presence of declines due to sperm limitation or decreased fertilization rate will not be limited to protogynous stocks. Although sperm production patterns and fertilization rates are not known for many commercially important species, this information can be collected to develop a general sense of how sperm production depends on individual size. We also have a general sense of the factors that are expected to affect fertilization rates (Birkhead and Møller, 1998) and these can be easily studied in any species where spawning grounds are accessible to researchers. It is clear that new management measures must be developed for sex-changing species that consider the potential for sperm limitation because biomass alone may miss the potential for rapid population crashes. One purpose of theory is to tell us what we need to know more about and to stimulate further research. Our results clearly indicate that we need to know more about sperm production and fertilization rates when managing protogynous stocks.

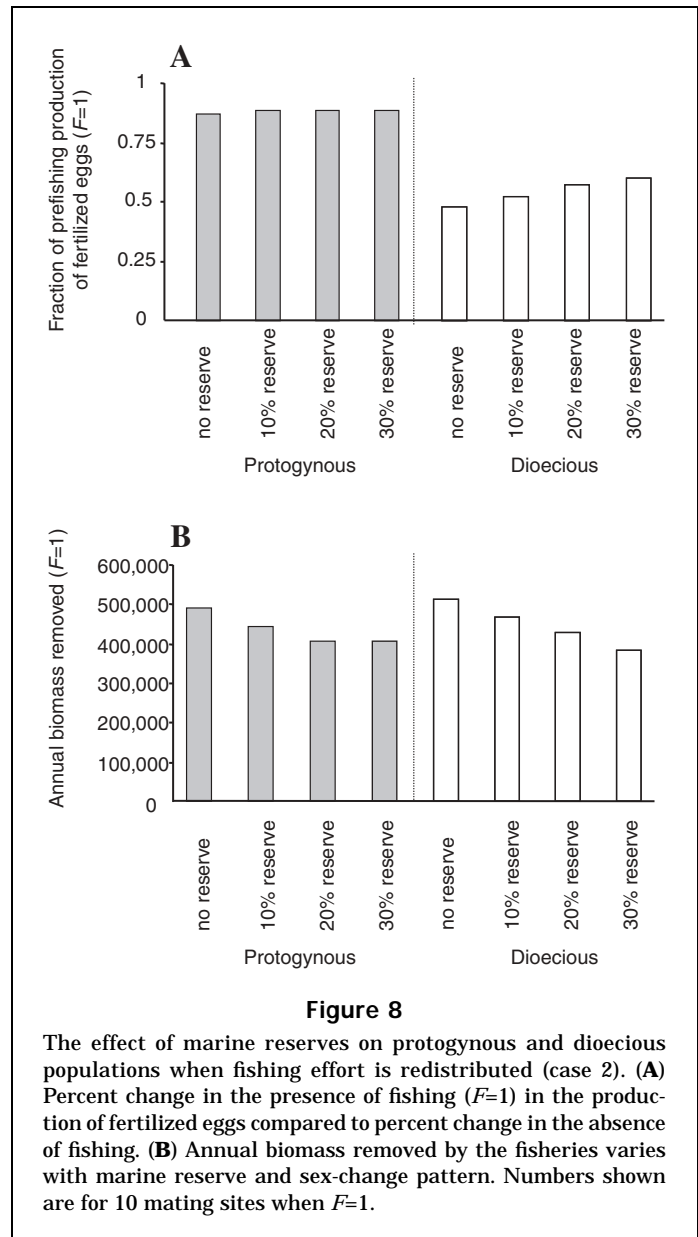


Figure 8

The effect of marine reserves on protogynous and dioecious populations when fishing effort is redistributed (case 2). (A) Percent change in the presence of fishing ($F=1$) in the production of fertilized eggs compared to percent change in the absence of fishing. (B) Annual biomass removed by the fisheries varies with marine reserve and sex-change pattern. Numbers shown are for 10 mating sites when $F=1$.

Marine reserves and size-selective fishing can be used to manage protogynous stocks

Marine reserves clearly have the potential to decrease the impact of fishing on populations. Large highly fecund or fertile individuals may be protected from size-selective fisheries. However, the benefits of a marine reserve will be significantly decreased if fishing effort is simply redistributed to unprotected sites (Figs. 7 and 8; Guenette and Pitcher, 1999; Apostolaki et al., 2002). It is usually recognized that the larval export and import dynamics will be crucial to whether reserves increase mean population size. We predict that the degree to which stocks respond to no-take reserves will also depend on their life-history pattern, mating system, and size-dependent fecundity and fertility. The protection of large and fecund (or fertile)

fish will certainly increase reproduction and decrease the impact of fishing on the population. However, the benefit of marine reserves will be much greater in populations where larger or older individuals play a key role in reproduction. Given the predicted extreme sensitivity of the protogynous population to the pattern of size-selective fishing, marine protected areas could represent a precautionary management strategy to ensure that some males are not subject to fishing mortality.

A comprehensive approach to stock dynamics

Managing fishing on stocks of sex-changing fish will require considering the sex-change pattern. However, one must also consider the sex change pattern within the context of the mating system. Although the pattern of sex determination does affect the stock dynamics, simple statements regarding whether dioecious or sex-changing populations are more sensitive to fishing are not possible. The differences among dioecious and sex-changing stocks are complex, and the management of these stocks will depend as much on their mating system, the type of fishing strategies used to capture them, and mating aggregation size as on the sex determination pattern. Classic SPR measures cannot measure sperm limitation and reduced fertilization rates, and thus will not always measure or predict the impact of fishing mortality on the population. Rather than relying on measures of spawning stock biomass per recruit alone, management groups should also monitor protogynous sex-changing stocks for a reduction in fertilization rates

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