

Predicting the effects of exploitation on male-first sex-changing fish

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Abstract

Sex change is widespread among tropical marine fishes, many of which are targeted by fisheries. Conservation concerns have been raised that sex-changing species may be particularly prone to overexploitation by size-selective fishing. In the case of male-first sex-changers, populations may become egg limited if large females are disproportionately killed. However, if males reduce the size at which they change sex in response to higher female mortality, the population may still be sufficiently productive. We develop an age-based model to explore the effects of fishing on two types of male-first sex-changing fish: one with flexibility in size-at-sex-change and one without. These effects were compared with those of non-sex-changing populations with similar life-history and population characteristics. The model predicts that if male-first sex-changers cannot respond to elevated female mortality by adjusting their size-at-sex-change, the population will be more prone to recruitment limitation and extinction than non-sex-changers. These effects will be amplified as smaller individuals become susceptible to fishing mortality. However, if size-at-sex-change is flexible, sex-changers may be as resilient to fishing as non-sex-changers. Knowledge of a species' size-at-sex-change, and the mechanisms controlling it, should be fundamental to the selection of fisheries conservation strategies.

Introduction

Sex change is widespread among marine fishes, especially in tropical regions (Atz, 1964; Devlin & Nagahama, 2002). Many sex-changing species support commercially important fisheries (e.g. groupers, wrasses, porgies, barramundi and shads). It has been hypothesized that sex-changers may fare worse under fisheries exploitation than non-sex-changers. This prediction, which has generated much conservation concern (e.g. Vincent & Sadovy, 1998; Côté, 2003; Alonzo & Mangel, 2004), stems from the fact that fishing generally removes the largest individuals from a population. In sex-changing species, size-selective fisheries therefore tend to disproportionately remove individuals of the larger sex. Because sex change is usually socially controlled (Shapiro, 1979, 1980; Ross, 1990; Mackie, 2003), it may be triggered earlier in response to the removal of individuals of the second sex, which could compensate for sex-selective fishing (Vincent & Sadovy, 1998). However, if compensatory sex change is insufficient to buffer skewed sex ratios, the scarcity of individuals of the second sex may reduce the reproductive output of a closed population to the point of population collapse (Jennings & Lock, 1996; Vincent & Sadovy, 1998).

Although male-first sex-change is the less common form of sex change among fishes (Atz, 1964), many species with

this reproductive mode are targeted by fisheries [e.g. barramundi *Lates calcarifer*, common snook *Centropomus undecimalis*, shads (*Tenualosa* spp.) and porgies (Sparidae)] (Yeung & Chan, 1987; Guiguen *et al.*, 1994; Milton *et al.*, 1997; Tobin, Sheaves & Molony, 1997; Blaber *et al.*, 1999; Taylor *et al.*, 2000). For these species, size-selective fishing may lead to male-biased sex ratios and population reproductive output may become egg limited. Fu, Quinn & Shirley (2001) provide the only comparison of the predicted effects of fishing on male-first sex-changers versus non-sex-changers: sex-changing *Pandalus* shrimp populations were predicted to be more vulnerable to recruitment overfishing than hypothetical non-sex-changing populations. However, this prediction assumed inflexibility in size-at-sex-change, despite the fact that plasticity in size-at-sex-change is known in pandalid shrimps (Charnov & Anderson, 1989; Koeller, Mohn & Etter, 2000; Wieland, 2004).

Incorporating flexibility in size-at-sex-change into fisheries models is important for predicting the effects of fishing on female-first sex-changers. Such flexibility buffers sex ratios under conditions of size-selective fishing (Huntsman & Schaaf, 1994; Alonzo & Mangel, 2005). The implications of such plasticity for male-first sex-changers remain unknown. Male-first sex-change can take either weeks or months depending on the species (e.g. Moore, 1979; Chang

& Yueh, 1990; Godwin, 1994b). If size-at-sex-change is flexible, and sex change can quickly replace fished females, egg production will be maintained for longer. However, we would still expect a decline in population reproductive output with a reduction in mean body size due to fishing, as would occur in populations of non-sex-changers.

In this study we use age-based simulations to compare the predicted responses to fishing of male-first sex-changing and non-sex-changing populations. We also explore the importance of considering flexibility in size-at-sex-change. Finally, we investigate the sensitivity of our predictions to the size selectivity of the fishery, flexibility in size-at-maturity, the strength of recruitment limitation at low population sizes and stochastic variation in recruitment. Our results provide predictions relating to the successful management of male-first sex-changing species, and raise questions regarding the conservation significance of sex change.

Methods

Sex-change scenarios

We used age-based simulations to investigate the effects of fishing on non-sex-changers, and sex-changers with and without flexibility in length-at-sex-change (see Appendix S1). To investigate the effects of reproductive mode *per se* on vulnerability to overfishing, we modelled non-sex-changing populations that were as comparable as possible to sex-changing populations by using the same life-history parameter values. We explored the effects of fishing on female and male biomass, the proportion of eggs fertilized and recruitment. We modelled scenarios with different levels of size selectivity by the fishery, different strengths of recruitment limitation, and flexible and inflexible length-at-maturity both with and without a stochastic element to recruitment. Finally, we compared the effects of fishing under a 'worst-case' scenario of strong recruitment limitation and where very small individuals were vulnerable to fishing.

We allowed individuals of different ages to differ in body size, natural mortality and reproductive output, and for sex-changers, gender. Population size was determined by natural and fishing mortality, reproductive output and recruitment. Reproductive output was a product of population size and sex ratio, and individual body size and reproductive mode. We chose to incorporate these complexities into our model in an attempt to capture the biological nature of marine fisheries and allow realistic fisheries-related predictions. All populations were seeded with 10 immature individuals in each age class and populations were limited to a carrying capacity of 900 individuals. Preliminary analyses showed that unfished populations stabilized after *c.* 15 years (represented by 15 model iterations). Each population was allowed 100 iterations to equilibrate before introducing fishing mortality. After a further 100 iterations to ensure equilibrium was reached, we investigated the effects of fishing on several variables that described the population dynamics. To measure the impact of fishing, we compared

the geometric mean of each variable from a time series of 50 iterations (equivalent to years) to the geometric mean from 50 iterations during a population's unfished state. All simulations were performed using MatLab 6.5.1 (MATLAB, 2003).

Parameter values

To parameterize the model, we used data derived from the male-first sex-changing white seabream *Diplodus sargus* (Mann & Buxton, 1998). More applicable data were available for this species than for any other male-first sex-changing fish species. As no data were available on the fertilization dynamics of any male-first sex-changer, we assumed a similar fertilization curve reported by Warner *et al.* (1995) for a female-first sex-changing wrasse. We used the same default values in all simulations except when investigating how varying a particular parameter affected a population's sensitivity to overfishing (see Table 1).

Growth and weight

Growth rate remained constant both before and after maturity. The length of an individual of age a , $L(a)$, was calculated using a von Bertalanffy equation where L_{inf} represents the asymptotic length (cm), k is growth rate and a_0 is the modelled age at which an individual is 0 cm [Eqn. (1)]:

$$L(a) = L_{\text{inf}}(1 - \exp^{-k(a-a_0)}) \quad (1)$$

As we assumed discrete age classes, growth between age classes was also assumed to be discrete.

We assumed that weight at age a , $W(a)$, differed between sexes (Pajuelo & Lorenzo, 2004) and was related to $L(a)$ by the equation $W(a) = gL(a)^h$, where g and h are sex-specific constants (see Table 1).

Natural and fishing mortality

Survival of individuals of age a after natural mortality at time t , $N_{(a)(t)}$, was calculated using Eqn. (2), where $N_{(a-1)(t-1)}$ is the number individuals of age $a-1$ at time $t-1$, and M is the instantaneous rate of natural mortality (see Table 1):

$$N_{(a)}(t) = N_{(a-1)}(t-1) \exp^{-M} \quad (2)$$

We assumed that natural mortality was twice as high for immature as for mature individuals (Planes, Jouvenel & Lenfant, 1998; Pajuelo & Lorenzo, 2004). Because few data are available on density-specific mortality rates for a range of adult ages, we assumed that M was density independent (see Table 1).

We modelled a size-selective fishery where fishing mortality increased with size up to a maximum of F_{MAX} . We used a logistic equation to calculate the proportion of F_{MAX} suffered by fish of length L , $p_F(L)$ [Eqn. (3)]:

$$p_F(L) = \frac{1}{1 + \exp^{-r(L-L_F)}} \quad (3)$$

Table 1 Descriptions and values of parameters used in simulations

Parameter	Value	Description and reference
<i>Growth</i>		
a_{MAX}	8+	Maximum age (years). Pajuelo & Lorenzo (2004) report that c. 95% of individuals occurred in ages 0–7
L_{inf}	45.9	Asymptotic body length. Average of Pajuelo & Lorenzo (2004), Gordo & Moli (1997), Martínez & Villegas (1996) and Man-Wai & Quingard (1984)
K	0.171	Von Bertalanffy growth rate. Average of Pajuelo & Lorenzo (2004), Gordo & Moli (1997), Martínez & Villegas (1996) and Man-Wai & Quingard (1984)
a_0	−0.87	Modelled Von Bertalanffy age (years) at which length is 0. Average of Pajuelo & Lorenzo (2004), Gordo & Moli (1997), Martínez & Villegas (1996) and Man-Wai & Quingard (1984)
<i>Weight</i>		
g_m	2.9×10^{-5}	Constant in the male length–weight relationship (length, mm) (Pajuelo & Lorenzo, 2004)
h_m	2.92	Exponent in the male length–weight relationship (length, mm) (Pajuelo & Lorenzo, 2004)
g_f	1.6×10^{-5}	Constant in the female length–weight relationship (length, mm) (Pajuelo & Lorenzo, 2004)
h_f	3.04	Exponent in the female length–weight relationship (length, mm) (Pajuelo & Lorenzo, 2004)
<i>Maturity</i>		
L_{MAT}	20.1	Length (cm) at which probability of maturation is 0.5 (Pajuelo & Lorenzo, 2004)
q	0.37	Slope of the maturity function. Estimated from Mann & Buxton (1998)
<i>Sex change</i>		
L_S	$0.8L_{a(OLDEST)}$	Size at which probability of sex change is 0.5. L_S in Mann & Buxton (1998) c. 80% maximum observed size. $L_{a(OLDEST)}$ is the length of the current oldest individual(s)
p	0.37	Steepness of sex change probability curve
<i>Reproduction</i>		
a	0.01	Constant in the egg production equation. Based on Pajuelo & Lorenzo (2004)
b	5.10	Exponent in the egg production equation. Based on Pajuelo & Lorenzo (2004)
c	$10^{-3}a$	Constant in the sperm production equation
d	b	Exponent in the sperm production equation
κ	30	Slope of the fertilization function. Based on Warner <i>et al.</i> (1995)
χ	0.09	Intercept of the fertilization function. Based on Warner <i>et al.</i> (1995)
<i>Population dynamics</i>		
N_{MAX}	900	Population carrying capacity
α	1.8×10^{-3} (1.8×10^{-2} , 3×10^{-4} , 1.5×10^{-4})	Density-independent larval mortality. Values in parentheses used to simulate low, strong and very strong recruitment limitation. The default value was used to simulate intermediate recruitment limitation
β	$\frac{\alpha}{0.667N_{MAX}}$	Recruitment function parameter
σ^2	0.1	Standard deviation of stochastic element in recruitment
<i>Natural and fishing mortality</i>		
F_{MAX}	0–2.5	Maximum instantaneous rate of fishing mortality (year^{-1})
L_F	28 (24, 32)	Length (cm) at which individuals suffer $0.5F_{MAX}$
R	0.37	Steepness of the fishing selectivity curve
M_{MAT}	0.3	Instantaneous rate of mortality (year^{-1}) for mature individuals. Based on Pajuelo & Lorenzo (2004)
M_{IMM}	$2 \times M_{MAT}$	Instantaneous rate of mortality (year^{-1}) for immature individuals

Where multiple values are given the default value is shown outside parentheses while those inside were used in specific simulations.

The slope of the selectivity curve described by Eqn. (3) is determined by r , and the length at its midpoint (i.e. the length at which individuals suffered a fishing mortality of $0.5F_{MAX}$) is determined by L_F . Thus, length-specific fishing mortality was calculated as $p_F(L)F_{MAX}$. We investigated the effect of changing the smallest catchable size by using low, intermediate or high values of L_F (24, 28 and 32 cm, respectively; see Table 1). This allowed us to explore the effects of different levels of exploitation on pre-sex-changed individuals. As a default, we assumed that the smallest catchable size occurred at an intermediate length. The number of surviving individuals of length L after annual

fishing mortality, $N_S(L)$, was calculated using Eqn. (4), where $N(L)$ is the number of individuals of length L before fishing:

$$N_S(L) = N(L) \exp^{-p_F(L)F_{MAX}} \quad (4)$$

Maturity

The proportion of individuals that mature, $p_{MAT}(L)$, was modelled using a length-based logistic equation [Eqn. (5)]. We let L_{MAT} be the size at which 50% of individuals mature, while q determined the slope of the curve. In a sex-changing

population all individuals matured as males; in non-sex-changing populations, the number of individuals maturing as males and females was determined using a set sex ratio (see the next section):

$$p_{\text{MAT}}(L) = \frac{1}{1 + \exp^{-q(L-L_{\text{MAT}})}} \quad (5)$$

The onset of maturation in many fish species is controlled socially (e.g. Kolluru & Reznick, 1996; Kuwamura, Nakashima & Yogo, 1996; Aday, Wahl & Philipp, 2003; Hobbs, Munday & Jones, 2004). Therefore, we investigated the importance of shifts in size-at-maturity in response to the size of other individuals in the population in both sex-changing and non-sex-changing populations. To simulate such flexibility, L_{MAT} was set at 56% of the largest individual in the population, reflecting the ratio of L_{MAT} to the modelled length-at-maximum-age (35.83 cm).

Sex change and sex ratios of non-sex-changing populations

For sex-changing populations, we calculated the proportion of males that changed sex, $p_S(L)$, using a length-based logistic regression [Eqn. (6)]. We let L_S be the length at which 50% of males have changed sex (henceforth, length-at-sex-change), while p determined the slope of the curve:

$$p_S(L) = \frac{1}{1 + \exp^{-p(L-L_S)}} \quad (6)$$

Sex-change reversal is rare in fishes, particularly among male-first sex-changers, and is poorly understood. Here we assumed that once an individual had changed sex, it remained female.

In populations with flexible length-at-sex-change (L_S), we assumed that L_S was controlled by the length of other individuals in the population (Shapiro, 1981; Ross, 1990). We assumed invariance in L_S relative to the length of the largest individual in the population (Charnov & Skúladóttir, 2000). Increases in fishing pressure cause declines in the age of the oldest individual in a population ($L_{a(\text{OLDEST})}$). Because individuals of the same age are assumed to be the same length [Eqn. (1)], fishing-mediated declines in the oldest age reached by any individual are accompanied by stepwise reductions in $L_{a(\text{OLDEST})}$. Length-at-sex-change was calculated as $0.80L_{a(\text{OLDEST})}$ and follows a similar stepwise decline with increasing F_{MAX} . We used 80% because sex change occurs at approximately this value in the white seabream (Mann & Buxton, 1998) and in sex-changing shrimps (Charnov & Skúladóttir, 2000). This variation of Charnov & Skúladóttir's (2000) model provides a computationally simple and biologically reasonable way of describing a fish's ability to detect and respond to a known cue for sex change. Further, Alonzo & Mangel (2005) showed that the specific mechanism used to model flexibility in size-at-sex-change had relatively little impact on expected effects of fishing compared with modelling sex-changing populations with fixed size-at-sex-change. For

populations with inflexible size-at-sex-change, L_S was calculated as 80% of the length reached at age a_{MAX} (Table 1).

In non-sex-changing populations, we calculated the proportion of individuals maturing as males using the average sex ratio of all stabilized, unfished sex-changing populations: 1.273 (male/female, as derived from preliminary simulations). Because the standard deviation in sex ratio between sex-changing scenarios was very small (± 0.012), this ratio provided a good baseline for comparison to all sex-changing populations.

Reproduction

Reproductive output of males and females increases allometrically with size. The number of eggs produced by females of length L , $E(L)$, was calculated as $E(L) = aL^b$, where a and b are constants (see Table 1). Similarly, the number of sperm (in millions) produced by males of length L , $S(L)$, was calculated as $S(L) = cL^d$, where c and d are constants (see Table 1). As discussed by Alonzo & Mangel (2004), the relationship between male size and fertility is poorly understood. We adopted their approach and assumed an allometric increase in sperm production with body size, where sperm production increased at the same rate as female egg production ($b = d$ above). However, as concerns regarding the overexploitation of male-first sex-changers focus on the potential for egg limitation, we also assumed that males were able to produce many more sperm than the number of eggs produced by females so that sperm limitation was unlikely. Furthermore, there is good evidence that males of species with sperm competition overproduce sperm to increase their competitive success rather than in response to fertility demands (Stockley *et al.*, 1997).

Mating was assumed to be an annual event and random with respect to size, as is the case in many species with external fertilization and that spawn in large mixed groups. Therefore, during mating the sperm and eggs produced by all individuals were pooled to give a total number of eggs, N_{EGGS} , and sperm, N_{SPERM} . The proportion of all fertilized eggs, p_E , increases to an asymptote with increasing sperm availability. This was described using Eqn. (7), where κ and χ are constants; their values suggest sperm limitation only when sex ratios were extremely female biased (see Table 1). Thus, the number of fertilized eggs, N_{FERT} , was $p_E N_{\text{EGGS}}$:

$$p_E = \frac{N_{\text{SPERM}}}{(\kappa N_{\text{EGGS}} + \chi) + N_{\text{SPERM}}} \quad (7)$$

Recruitment

The Beverton–Holt function (Beverton & Holt, 1957) describes the number of larval recruits produced, N_{PR} , as a function of the number of fertilized eggs. However, the number of larvae produced by this relationship was constrained to ensure that the population did not exceed its carrying capacity of 900 individuals, N_{MAX} . Therefore, the number of actual recruits, N_{R} , was dictated by the space

available in the population, if any [Eqn. (8)]:

$$N_R = \begin{cases} N_{PR} = \frac{\alpha N_{FERT}}{1 + \beta N_{FERT}} & \text{if } \frac{\alpha N_{FERT}}{1 + \beta N_{FERT}} + \sum_{a=1}^{a=N_{MAX}} N_a > N_{MAX} \\ N_R = \max\left(0, N_{MAX} - \sum_{a=1}^{a=N_{MAX}} N_a\right) & \text{if } \frac{\alpha N_{FERT}}{1 + \beta N_{FERT}} + \sum_{a=1}^{a=N_{MAX}} N_a \leq N_{MAX} \end{cases} \quad (8)$$

Equation (8) captures both density-dependent and density-independent processes that determine recruit survival. Density-dependent processes include competition for resources, density-independent processes include environmental variables such as temperature, and both are likely to vary greatly between areas. In Eqn. (8), α determined the strength of density-independent recruitment limitation, β was the level of density-dependent larval survival and N_a was the number of individuals at age a ; α and β were fitted so that the asymptotic number of larvae was two-thirds of the population carrying capacity. We used this value because preliminary investigations revealed that it allowed both density-dependent and density-independent recruitments to occur given the population sizes simulated. We explored the effects of differing strengths of recruitment limitation at small population sizes by using different values of α to alter the rate of increase to the asymptote (see Table 1). In our default model, the strength of recruitment limitation was assumed to be intermediate ($\alpha = 0.0018$).

We repeated our simulations to investigate the importance of stochasticity in recruitment. After calculating the number of larvae, a proportion of these larvae was added or removed as defined by ε , which was a random number between -1 and 1 taken from a normal distribution with a mean of 0 and a standard deviation, σ^2 , of 0.1 .

A feature of our model is that fishing-mediated changes in female biomass and in the number of fertilized eggs in sex-changing populations with flexible L_S are not smooth declines. This is caused by the stepwise decline in age-at-sex-change, which results in many more (smaller) females arising from sex change under high F_{MAX} than under a slightly lower F_{MAX} . The increase in number of females causes a slight, short-lived net increase in female biomass despite a decline in average female size. As fishing increases further, female biomass and the number of fertilized eggs fall again until a further stepwise decline in size-at-sex-change occurs.

Results

Male-first sex-changer response to fishing

All sex-changing and non-sex-changing populations show a rapid decline in female biomass. This decline was greatest in sex-changing populations without flexibility in length-at-sex-change. Decline in female biomass was smallest in non-sex-changing populations (Fig. 1c) and intermediate in sex-changing populations exhibiting flexibility in L_S (Fig. 1a). Only non-sex-changing populations showed a

decline in male biomass that was comparable to that of females (Fig. 1c).

The declines in female biomass were reflected in the number of eggs fertilized, relative to pre-fishing values. In all sex-changing and non-sex-changing populations, egg production was sensitive to fishing effects. The proportion of eggs fertilized (relative to pre-fishing values) showed a marked decline even at low F_{MAX} , reflecting the loss of the most fecund females. The number of eggs fertilized in all populations declined by different extents: sex-changing populations with no flexible length-at-sex-change (L_S) showed the greatest decline (percentage of pre-fishing geometric mean at highest F_{MAX} simulated = 7%) while non-sex-changing populations showed the least sensitivity

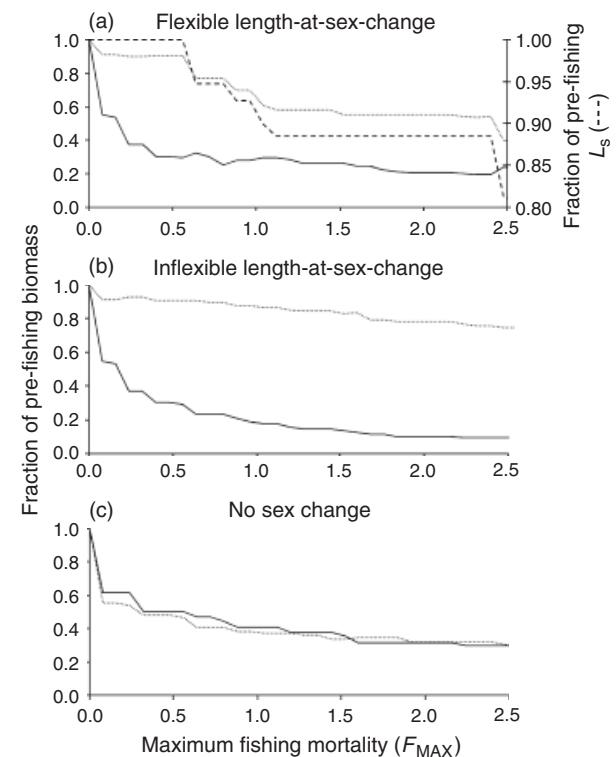


Figure 1 Fishing-mediated changes in female (solid lines) and male (dotted lines) biomass for (a) sex-changers with flexible length-at-sex-change, L_S , (b) sex-changers with inflexible L_S and (c) non-sex-changers. The equilibrium fraction of pre-fishing L_S is shown in (a) for the sex-changing population with flexible L_S (dashed line). Simulations were performed with intermediate strength of recruitment limitation ($\alpha = 0.0018$), and smallest catchable size set at an intermediate length ($L_F = 28$ cm). Note: simulations involved no stochastic element in recruitment and inflexible size-at-maturity.

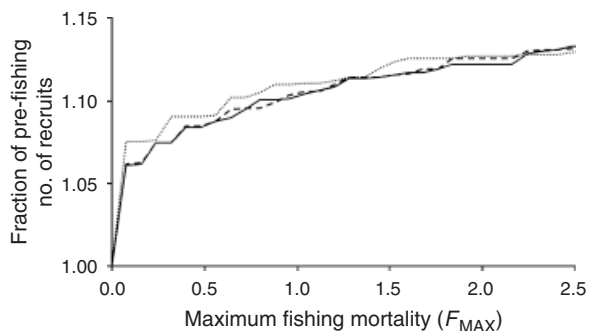


Figure 2 Fishing-mediated changes in number of recruits for non-sex-changers (dotted line), sex-changers with flexible length-at-sex-change, L_S (solid line), and sex-changers with inflexible L_S (dashed line). Simulations were performed with intermediate strength of recruitment limitation ($\alpha=0.0018$), and smallest catchable size set at an intermediate length ($L_F=28$ cm). Also, see note in Fig. 1.

(18%). Sex-changing populations with flexible L_S showed an intermediate response (15%).

Despite declines in the proportion of eggs fertilized, all populations showed similar increases in annual recruit survival as fishing mortality increased (Fig. 2). Increased adult mortality due to fishing provided potential recruits with more habitat and space and an opportunity to join the adult population, despite the low probability of their future survival as adults.

Similar patterns in female biomass, production of fertilized eggs and recruits were obtained when we allowed flexibility in size-at-maturity (L_{MAT}) and added a stochastic element to recruitment (results not shown).

Fishing size selectivity

The impact of fishing was greatest for all populations when the smallest catchable size was less than length-at-sex-change (L_F less than L_S ; Fig. 3). When only large individuals could be caught (Fig. 3a), non-sex-changing populations showed smaller declines in female biomass than both sex-changing populations at all fishing mortalities. When small individuals were susceptible to fishing mortality (Fig. 3b), males in populations without flexible L_S suffered high levels of fishing mortality compared with populations with flexible L_S . As a result, sex-changing populations without flexible L_S showed the greatest declines in female biomass and were nearly extirpated at high F_{MAX} .

Recruitment limitation

Changes in the strength of density-dependent recruitment affected the fraction of pre-fishing female biomass in all populations. In turn, this altered the ability of these populations to produce a sustainable number of recruits as fishing mortality increased (Fig. 4). Populations without flexible L_S were most sensitive to increases in levels of recruitment limitation. Under conditions of very strong recruitment limitation, the number of spawning females declined

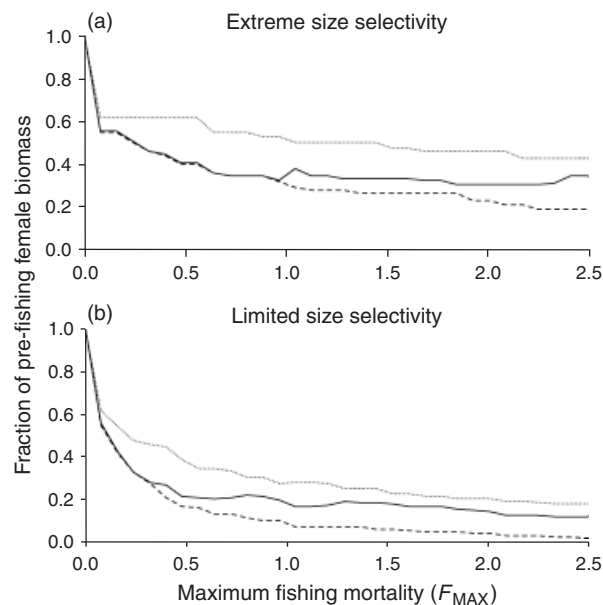


Figure 3 Fishing-mediated changes in female biomass under different fishing size-selectivity regimes: (a) extreme size-selectivity: only large individuals were catchable ($L_F=32$ cm) and (b) limited size-selectivity: even small individuals were catchable ($L_F=24$ cm), for non-sex-changers (dotted lines), sex-changers with flexible size-at-sex-change, L_S (solid lines), and sex-changers without flexible L_S (dashed lines). Simulations were performed with intermediate strength of recruitment limitation ($\alpha=0.0018$). Also, see note in Fig. 1.

severely and these populations were extirpated at high F_{MAX} (Fig. 4c). Recruitment limitation only affected the fraction of pre-fishing female biomass of populations with flexible L_S when recruitment limitation was very strong and F_{MAX} was very high (compare Figs 4a–c). Non-sex-changing populations were also only affected when recruitment limitation was very strong, but under these conditions they showed greater sensitivity to increases in fishing mortality than populations of sex-changers with flexible L_S (Fig. 4c).

Worst-case scenario: small individuals susceptible to fishing and strong recruitment limitation

Under the most extreme scenario simulated, populations without flexibility in length-at-sex-change showed poor ability to withstand fishing and were extirpated at relatively low fishing mortality (*c.* $F_{MAX}=1$; Fig. 5). At low to intermediate levels of fishing mortality, non-sex-changing populations were most resilient. However, at very high F_{MAX} (>2.4), sex-changing populations with flexible L_S exhibited similar declines in female biomass to non-sex-changing populations.

Discussion

We explored the effects of fishing on male-first sex-changing populations compared with non-sex-changers under varying

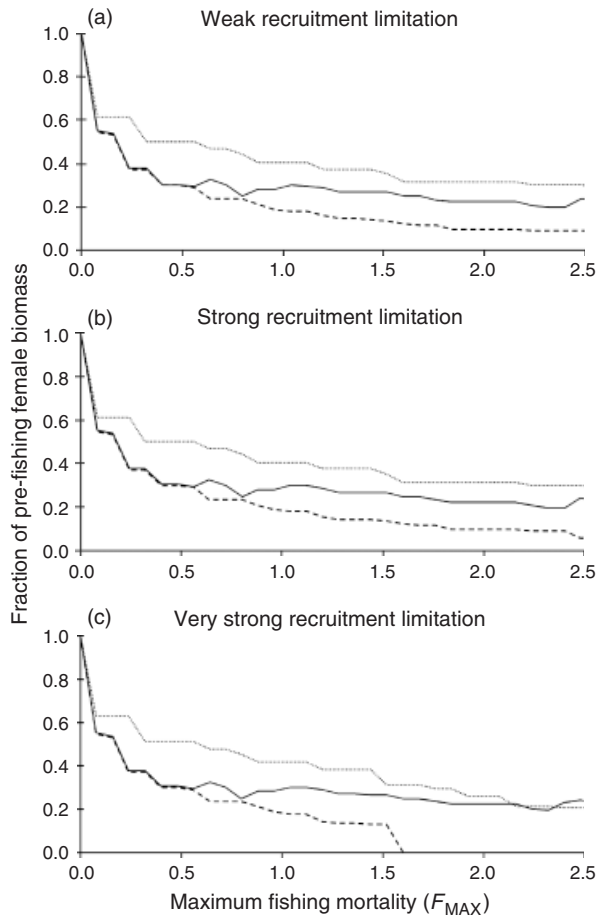


Figure 4 Fishing-mediated changes in female biomass under different density-independent recruitment limitation scenarios: (a) weak recruitment limitation ($\alpha=1.8 \times 10^{-2}$), (b) strong recruitment limitation ($\alpha=3.0 \times 10^{-4}$) and (c) very strong recruitment limitation (1.5×10^{-4}) for non-sex-changers (dotted lines), sex-changers with flexible length-at-sex-change, L_S (solid lines), and sex-changers with inflexible L_S (dashed lines). Simulations were performed with smallest catchable size set at an intermediate length ($L_F=28$ cm). Also, see note in Fig. 1.

conditions of recruitment, smallest catchable sizes and fishing mortality. Sex-changing populations without flexibility in their length-at-sex-change (L_S) were more susceptible to recruitment overfishing and extirpation than sex-changers with flexible L_S or non-sex-changers. Sex-changers without flexible L_S showed the most marked declines in female biomass and proportion of eggs fertilized with increasing fishing mortality. These effects were exacerbated when the fishery caught pre-sex-changed fish. However, these declines only translated to population extirpation when recruitment was limiting at small population sizes. Furthermore, the greater susceptibility of sex-changers to extirpation disappeared if sex-changers could adjust their size-at-sex-change.

Several of our predictions are similar to those made by other simulations of the impacts of fishing on male-first sex-changers. For instance, Milton *et al.* (1998) also predicted that size-selective fishing of the commercially important,

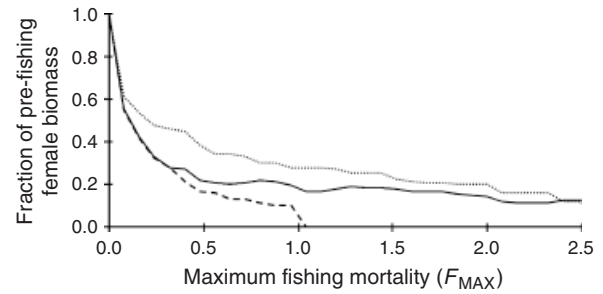


Figure 5 Fishing-mediated changes in female biomass under a worst-case scenario with strong recruitment limitation ($\alpha=3.0 \times 10^{-4}$) and where small individuals were catchable ($L_F=24$ cm) for non-sex-changers (dotted line), sex-changers with flexible L_S (solid line) and sex-changers with inflexible L_S (dashed line). Also, see note in Fig. 1.

male-first sex-changing barramundi will cause rapid declines in female biomass, which could lead to egg-limited recruitment. Likewise, the prediction that sex-changers without flexible size-at-sex-change should be more sensitive to overfishing than non-sex-changers is consistent with simulations by Fu *et al.* (2001) in a study of *Pandalus* shrimps. These similarities demonstrate that, despite predominantly basing the parameters of our model on a specific species, the general patterns we predict are probably applicable to a range of male-first sex-change systems.

The general applicability of our predictions is particularly significant as previous simulations of the impacts of fishing on male-first sex-changers have ignored the importance of flexibility in size-at-sex-change. For example, despite strong evidence that *Pandalus* shrimps exhibit plasticity in their size-at-sex-change (Charnov & Skúladóttir, 2000; Koeller *et al.*, 2000; Wieland, 2004), Fu *et al.* (2001) assumed a fixed size-at-sex-change. Similarly, the effects of fishing on the barramundi predicted by Milton *et al.* (1998) were also based on the assumption that size-at-sex-change in this species is fixed. In light of our predictions, it would not be surprising if compensatory shifts in size-at-sex-change buffer the effects of fishing in pandalid shrimps and barramundi.

Our predictions regarding the relative sensitivity of male-first sex-changers and non-sex-changers to fishing also mirror predictions from similar models investigating female-first sex-changers. Generally, at high fishing mortality and assuming no flexibility in size-at-sex-change, female-first sex-changers are expected to suffer sperm limitation through the disproportionate removal of large males (Punt, Garratt & Govender, 1993), which makes these species more prone to overfishing than non-sex-changers (Bannerot, Fox & Powers, 1987; Huntsman & Schaaf, 1994; Côté, 2003; Alonzo & Mangel, 2004). However, Alonzo and Mangel (2005) predicted that if compensatory shifts in size-at-sex-change occur, these species should be as resilient to fishing as non-sex-changers.

Socially mediated flexibility in size-at-sex-change is common (Ross, 1990). However, the degree of flexibility probably varies naturally more than described by our simulated populations, which represent two extremes along a plasticity

continuum (inflexible vs. completely flexible). For example, different species change sex at different rates (e.g. Godwin, 1994a; Sakai *et al.*, 2003). Male-first sex-changers with slow gonadal metamorphosis may not be able to replace fished females fast enough to buffer completely the effects of fishing before the next reproductive bout. Similarly, if shifts in size-at-sex-change in response to fishing pressure are only possible over evolutionary timescales, flexibility in size-at-sex-change is unlikely to be sufficient to buffer the impacts of fishing. Slow shifts in size-at-sex-change are of particular concern when increases in fishing are large and sudden, such as during the opening of a new fishery or of an area that was formerly protected. Therefore, investigations into the speed at which sex change occurs in exploited species could help to predict resilience to fishing.

Removal of pre-sex-changed individuals from male-first sex-changing populations may be a particularly dangerous strategy as it would leave few, if any, females, which may lead to population egg limitation. In a commercially important fish, the male-first sex-changing barramundi, a decrease in the size of capture is predicted to impair recruitment severely (Milton *et al.*, 1998). However, as mentioned, Milton *et al.* (1998) assumed a fixed size-at-sex-change. If further research reveals that compensatory shifts in size-at-sex-change occur in barramundi (and gonadal metamorphosis is rapid), the ability of this species to recruit successfully may be greater than previously thought.

In summary, our comparison of the predicted effects of exploitation on male-first sex-changers and non-sex-changers indicates that male-first sex-change may increase vulnerability to overfishing if size-at-sex-change is inflexible. However, if size-at-sex-change is flexible, populations of male-first sex-changers may be as likely to crash as a result of overfishing as non-sex-changers. If our predictions are correct, measures to conserve exploited sex-changing stocks should consider size-at-sex-change and the mechanisms determining this size, and should ensure that fishing mortality on pre-sex-changed individuals is low.

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Supplementary material

The following material is available for this article online:

Appendix S1 A schematic description of the model.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-1795.2006.00065.x>

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