

## Original Article

# Evolutionary and demographic impacts of sex change rules and size-selective exploitation on sequential hermaphrodites

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Relatively few studies have addressed fishery-induced-evolution of sequential hermaphrodites although declines in the mean size-at-maturation and/or sex change have been documented for several species. We sought to explore the evolutionary impacts of size-selective exploitation on maturation and sex change of a protogynous hermaphrodite using an individual-based model accounting for growth, survival, maturation, sex change, and reproduction. Because sex change rules are unknown for many exploited species, critical size-at-sex change (static and genetic control) and social control of sex change were evaluated to determine how life-history-traits (maturation, sex change) and population reference points change due in part to evolution. When simulating critical size-at-sex change, mean length-at-maturation increased, contrary to typical predictions for dioecious species, and mean length-at-sex change decreased (when under genetic control) from exploitation. These changes occurred slowly and resulted in lower male: female sex ratios, sperm limitation, and extirpation at high exploitation rates. Under social control of sex change, both the mean lengths-at-maturation and sex change decreased relatively rapidly from exploitation. These populations maintained high male: female sex ratios, avoided sperm limitation, and withstood higher exploitation rates than critical size-at-sex change populations. Results from these models highlight the need for a better understanding of sex change rules for exploited hermaphrodites.

**Keywords:** exploitation, fishery-induced-evolution, individual-based-model, life-history evolution, maturation, sequential hermaphrodite, sex ratio, sexual transition

## Introduction

Intensive harvest along with the selective practices of many fisheries has been identified as a key driving force behind changes in the population structure and phenotypic traits of many exploited fish stocks (Rijnsdorp, 1993; Grift *et al.*, 2003; Olsen *et al.*, 2005). Observed phenotypic changes can be strictly demographic (e.g. we see no big fish because they have been preferentially removed) and/or have an evolutionary component (e.g. we see no big fish at least in part because growth rates have slowed as a result of evolution). Further, the selective practices of a fishery may result in the preferential removal of individuals that vary in phenotype in less obvious ways (e.g. more aggressive feeding, fast growth,

late maturation, etc.) and, to the extent these traits are heritable, fishing will result in the evolution of these traits as well (Law, 2000; Heino and Godø, 2002; Kuparinen and Merilä, 2007). Much of the work assessing the impacts of fishing on wild populations has been conducted on dioecious species, largely ignoring the impacts of exploitation on life-history-traits of sequential hermaphrodites, despite the fact that many harvested fish are hermaphroditic (but see Hamilton *et al.*, 2007; Collins and McBride, 2011; Fenberg and Roy, 2012; Mariani *et al.*, 2013).

Decreases in the mean lengths-at-maturation and sex change have been shown in many sequentially hermaphroditic species (e.g. hogfish *Lachnolaimus maximus*, California sheephead

*Semicossyphus pulcher*, *Lottia gigantea*, *Chrysoblephus puniceus*; Hamilton *et al.*, 2007; Collins and McBride, 2011; Fenberg and Roy, 2012; Mariani *et al.*, 2013). These changes may be indicative of an evolutionary response to harvest because life-history-traits generally have low but significant heritability (i.e. Mousseau and Roff, 1987; Roff, 1993; Weigensberg and Roff, 1996; Jónasson *et al.*, 1997; Conover and Munch, 2002). For other species (e.g. gag *Mycteroperca microlepis*, scamp *Mycteroperca phenax*, and red grouper *Epinephelus morio*), changes in the mean length-at-maturation and sex change have not been identified (Coleman *et al.*, 1996; SEDAR, 2014; Provost and Jensen, 2015). When maturation and/or sex change does not respond to changes in the population structure, populations can experience drastic changes in the male:female sex ratio (hereafter referred to as M:F sex ratio). For example, M:F sex ratios of gag declined from 17 to 1% and scamp declined from 36 to 18% over the course of 20 years (Coleman *et al.*, 1996). In extreme cases, this can lead to sperm or egg limitation from the loss of terminal sex individuals (Huntsman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004). The extent of these effects depends on how the sex change is controlled and can have very different outcomes depending on how sex change is initiated (Huntsman and Schaaf, 1994; Alonzo and Mangel, 2005).

The mechanisms controlling sex change are unknown for many exploited sequential hermaphrodites and many hypotheses have been developed to predict when sex change should occur. The hypothesis that a developmental process initiates sex change in fish (e.g. at a critical size or age) has been around for ~70 years (e.g. Liu, 1944), suggesting that for some species the size/age-at-sex change is likely directly genetically controlled. Work by Shapiro, Warner, Charnov and coauthors suggest that sex change should occur when individuals can improve their reproductive fitness (e.g. the size advantage model; Ghiselin, 1969) and often occurs in response to social cues, behavioural responses, or demographic changes (e.g. see Charnov, 1982b; Shapiro and Boulon, 1982; Warner, 1988). This suggests that the sex change is highly plastic and can change rapidly in response to changes in social conditions. These hypotheses predict very different evolutionary responses to fishing and can have large effects on the long-term sustainability of a population and fishery.

Whether sex change is initiated by a developmental process or responsive to social conditions, it is important to understand how alternative scenarios of sex change would influence changes in life-history-traits and alter population structure over the course of time in response to fishing pressure. When assuming static size/age-at-sex change, studies have consistently found that harvest leads to sperm limitation at high fishing mortality rates (Huntsman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004, 2005; Brooks *et al.*, 2008). When sex change varies in response to social conditions, studies predict decreases in the mean length-at-sex change and often little sperm limitation from exploitation over both short-term (i.e. over few generations; Huntsman and Schaaf, 1994; Alonzo and Mangel, 2005; Robinson *et al.*, 2017) and long-term evolutionary models (i.e. over tens to hundreds of generations; Sattar *et al.*, 2008). Likewise, the mean length-at-maturation is consistently predicted to decrease from exploitation in both short-term (Huntsman and Schaaf, 1994; Robinson *et al.*, 2017) and long-term evolutionary models (Sattar *et al.*, 2008). This trend in the mean length-at-maturation has also been identified in many empirical studies on hermaphroditic (e.g. Hamilton *et al.*, 2007; Collins and

McBride, 2011; Fenberg and Roy, 2012; Mariani *et al.*, 2013) and dioecious species (e.g. Rijnsdorp, 1993; Trippel, 1995; Conover and Munch, 2002; Olsen *et al.*, 2004, 2005; Mollet *et al.*, 2007; Pardoe *et al.*, 2009). The results of these studies show the importance of comparing multiple mechanisms controlling sex change and allowing the size/age-at-maturation to vary to fully understand the impacts of fishing on sequential hermaphrodites.

Up to this point, few studies have assessed the potential evolutionary consequences of fishing on sequential hermaphrodites. Sattar *et al.* (2008) used an optimization model to predict how the size/age-at-maturation evolves and sex change changes in response to various levels of fishing mortality. However, they did not compare the effects of different sex change rules and only applied the size advantage model. In this study, we expanded on the work by Huntsman and Schaaf (1994), Alonzo and Mangel (2005), and Sattar *et al.* (2008) by comparing how different rules of sex change influence the evolutionary response to selective harvest. Further, we did this by comparing the evolutionary trajectories of life-history-traits (e.g. the mean lengths-at-maturation and sex change) and population reference points [e.g. M:F sex ratio, spawning potential ratio (SPR), fertilization rate, and the probability of recruitment failure] through time. Our primary objective was to determine how the mean lengths-at-maturation and sex change of a sequential hermaphrodite can be expected to evolve under size-selective fishing mortality. Our secondary objective was to assess how mechanisms controlling sex change (e.g. critical size or social control) influence the evolutionary trajectories and the population-level response to size-selectivity and fishing pressure. The final objective was to determine which mechanisms driving sex change are likely the most susceptible to overfishing and fishery-induced-evolution.

## Methods

We used an individual-based model representative of a large, long-lived protogynous hermaphrodite (e.g. gag, red grouper, hogfish, California sheephead) to determine the effects of size-selective fishing on the evolutionary trajectories of life-history-traits and temporal trends in population reference points. In this model, fish experienced growth, size-based natural and fishing mortality, maturation, transition from female to male, and reproduction (see Supplementary Figure S1 for a flowchart). Maturation could evolve and sex change could also evolve or change as a result of social conditions. Heritability ( $h^2$ ) was assumed to equal 0.2 for both of these life-history-traits (Mousseau and Roff, 1987; Roff, 1993; Weigensberg and Roff, 1996; Jónasson *et al.*, 1997; Conover and Munch, 2002). Individuals were allowed to mature and transition to male in the same year, effectively bypassing female function and reproducing as a male for their entire adult life. This life-history strategy has been frequently observed in the families Labridae (Wrasses) and Scaridae (Parrotfishes; see Charnov, 1982a; Warner, 1982, 1984).

The mechanisms controlling sex change can have large effects on how sequentially hermaphroditic populations respond to size-selective fishing mortality (Huntsman and Schaaf, 1994; Alonzo and Mangel, 2005). Therefore, we considered the scenarios: (1) sex change was controlled by a developmental process (i.e. a critical size) and (2) determined via social control. Two critical size models were assessed: (1a) the critical size-at-sex change was held static, as is commonly assumed in assessment and population models used to inform management strategies (e.g. Alonzo and Mangel, 2004; Brooks *et al.*, 2008; SEDAR, 2014; Provost and Jensen, 2015) and

(1b) it was a heritable trait subject to evolution. For social control of sex change, the size advantage model developed by Ghiselin (1969) was used to determine which individuals transitioned to male. This model predicts that females transition to male when their reproductive success as a male is greater than if they remain female. We considered two social control scenarios; the models differed solely in the order of survival, maturation, and sex change to represent species in which (2a) males and females are well mixed throughout the year (i.e. maturation and sex change happen immediately prior to reproduction), as expected with Hogfish and Red Grouper (Coleman et al., 1996; Collins and McBride, 2011) and (2b) a lag between the maturation/sex change process and reproduction (i.e. mortality occurs between maturation/sex change and reproduction) as might occur if sexes are largely segregated except during reproduction, as is expected with gag (Coleman et al., 2011). This allowed us to determine how the mechanisms controlling sex change influenced the evolutionary trends in maturation and sex change, the temporal trends in population reference points and the sustainability of a population and fishery.

Simulations were run for 700 years with fishing starting in year 200. A range of fishing mortality rates ( $F=0.0, 0.1, \dots, 0.5$ ) were used and 100 replicates run for each sex change rule and fishing mortality rate. An additional set of simulations were run for 10000 years (with fishing starting in year 200) to verify trends identified in the 700-year simulation (results in Supplementary Material). Evolution in maturation and sex change were assessed via trends in the mean lengths-at-maturation and sex change. Trends in population reference points were assessed via changes in M:F sex ratio, SPR, fertilization rate, and the probability of recruitment failure. SPR was calculated as the ratio of fertilized eggs produced when unfished (i.e. year 199) to the number of fertilized eggs produced after fishing started and is an index of relative reproductive capacity in a given year. Fertilization rate was the proportion of eggs fertilized in a given year and was used to assess sperm limitation. The probability of recruitment failure was calculated as the proportion of simulations in which no recruits were produced in a given year. Results for SPR, fertilization rate, and the probability of recruitment failure can be found in the Supplementary Material. Detailed model description, expanded sensitivity analyses, and results for SPR, fertilization rate, and probability of recruitment failure are located in the Supplementary Material. Growth parameters (i.e. mean juvenile growth rate and female/male reproductive investment) were obtained for gag from Matthias et al. (2016) and are located in Supplementary Table S1.

**Basic model structure**

Juvenile growth rates ( $h_i$ ) and adult reproductive investment ( $g_{i,s_i}$ ) varied between individuals ( $i$ ), but for simplicity were not allowed to evolve over time and were density-independent. A tri-phasic growth model, developed by Matthias et al. (2016), was used to describe juvenile, female, and male-specific growth rates:

$$L_{i,y} = \begin{cases} 0, & \text{if } a = 0 \\ L_{i,y-1} + h_i, & \text{if } mat_i = 0 \\ L_{i,y-1} * e^{-k_{i,s_i}} + L_{\infty,i,s_i} * (1 - e^{-k_{i,s_i}}), & \text{if } mat_i = 1 \end{cases} \quad (1)$$

where  $L_{i,y}$  is the length of individual  $i$  in year  $y$ , length-at-age 0 ( $a = 0$ ) is zero,  $k_{i,s_i} = \ln(1 + g_{i,s_i}/3)$  is the stage-specific Brody growth coefficient (stages  $s_i = 1$  is juvenile/female and  $s_i = 2$  is

male), and  $L_{\infty,s_i} = 3h_i g_{i,s_i}^{-1}$  is the stage-specific asymptotic size. This model is an extension of the Lester et al. (2004) growth model where juvenile growth ( $mat_i = 0$ ) is linear and adult growth ( $mat_i = 1$ ) follows the von Bertalanffy model. Changes in adult growth after sex change correspond to greater male reproductive investment (i.e.  $g_{i,s_i=2} = 1.2 * g_{i,s_i=1}$ ) and thus changes in growth patterns (see Supplementary Figure S2 for sample growth trajectories and a length-at-age plot). As suggested by Matthias et al. (2016), changes in reproductive investment after sex change are likely caused by changes in aggression because more aggressive males often have a greater chance of defending mating opportunities, mating sites, or territories (Tecot et al., 2013; Georgiev et al., 2014).

Survival was a function of size-based natural mortality, a juvenile mortality component ( $M_{juv}$ ), and fishing mortality. A modified Lorenzen (2000) Supplementary Equation (S8) was used for size-based natural mortality where mortality decreased as a function of length. The parameter  $M_{juv}$  was applied to juveniles in addition to the size-based natural mortality rate and was a tuning parameter to set when individuals mature (initially set so that the mean length-at-maturation was approximately equal to 66% of the mean female  $L_{\infty}$ ). Greater mortality rates for juvenile fish could happen when the relative risk of predation decreases as individuals shift to different habitat after maturation, as is observed in many commercially important reef fish (e.g. gag, red grouper, scamp, hogfish; red snapper *Lutjanus campechanus*; Koenig and Coleman, 1998; Gallaway et al., 2009; Coleman et al., 2011; Collins and McBride, 2011). For instance, larval gag settle in shallow nearshore habitats, are found on shallow reefs as juveniles, and progressively migrate to deeper offshore reefs as they mature then transition to males (Koenig and Coleman, 1998; Coleman et al., 2011).

Length-at-maturation  $L_{mat,i,a}$  for individual  $i$  was modelled using a linear deterministic maturation reaction norm:

$$L_{mat,i,a} = \beta_{1,i} + \beta_{2,i} * a, \quad (2)$$

where  $\beta_{1,i}$  is the intercept representing length and  $\beta_{2,i}$  is the slope representing the age component. In all scenarios  $\beta_{1,i}$  and  $\beta_{2,i}$  evolve via inheritance. For the critical size-at-sex change scenarios, individuals change sex when their length is greater than  $\beta_{3,i}$  (the critical length-at-sex change). When sex change was under genetic control,  $\beta_{3,i}$  evolved. For the social control models, sex change followed the size advantage model and occurred when the number of eggs an individual could fertilize as a male exceeded the number of eggs that individual produced as a female.

Reproduction occurred at the end of the year and determined the number of recruits (following the Beverton–Holt stock–recruitment relationship) and the distribution of genetically controlled parameters via inheritance. Egg production  $\varphi_{i,y}$  for female  $i$  in year  $y$  was assumed to be proportional to length cubed times reproductive investment and sperm production  $\xi_{i,y}$  for male  $i$  in year  $y$  was assumed to be ten times greater than that of a similar female (arbitrarily set to represent small gamete size and account for low fertilization rate with external fertilization).

$$\begin{aligned} \varphi_{i,y} &= g_{i,s_i=1} * \alpha L_{i,y}^b \\ \xi_{i,y} &= 10 * g_{i,s_i=2} * \alpha L_{i,y}^b \end{aligned} \quad (3)$$

where  $\alpha$  and  $b$  are constants relating length to weight. A male size advantage parameter ( $\delta$ ) was used to represent the relationship between male size and access to females

$$\theta_{i,y} = \sum_{j=1}^{n_1} \varphi_{j,y} * L_{i,y}^{\delta} \left( \sum_{j^*=1}^{n_2} L_{j^*,y}^{\delta} \right)^{-1}, \quad (4)$$

where the first component is the total egg production by all  $j = (1, \dots, n_1)$  females alive in year  $y$ ,  $L_{i,y}$  is the length of male  $i$  in year  $y$ , and the component in parentheses prevents the total number of fertilized eggs from being greater than total egg production. When  $\delta > 0$ , larger males have greater access to females than smaller males and when  $\delta = 0$ , all males have equal access to females. Values for  $\delta$  were arbitrarily set at 1, 4, and 8 to represent various levels of male size advantages. We assumed sperm limitation occurred when egg production was less than sperm production.

The model assumed random mating and offspring were assigned parents in proportion to gamete production (for females) and fertilized eggs (for males). Inheritance for maturation ( $\beta_{1,i}$  and  $\beta_{2,i}$ ) and sex change ( $\beta_{3,i}$  when genetically controlled) was modelled following a modified breeder's equation:

$$\bar{\beta}_{x,i} = h^2 * \left( \text{mean}(\beta_{x,j_1}, \beta_{x,j_2}) - \bar{\beta}_{x,y} \right) + \bar{\beta}_{x,y} \quad (5)$$

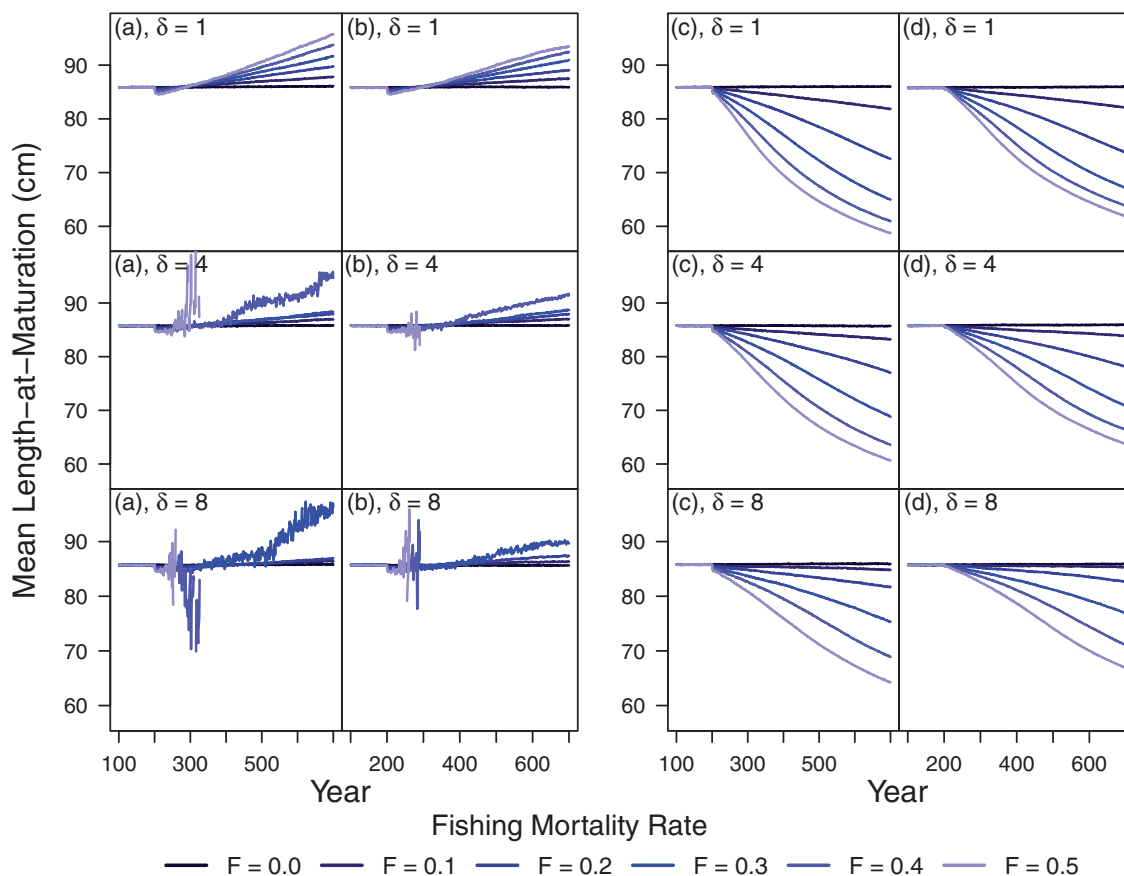
where  $\bar{\beta}_{x,i}$  is the predicted mean for offspring  $i$ ,  $\sigma_{\beta_x}$  is the standard deviation,  $\beta_{x,j_1}$  and  $\beta_{x,j_2}$  are the trait values for parents  $j_1$

and  $j_2$ ,  $\bar{\beta}_{x,y}$  is the fecundity-weighted mean  $\beta_x$  in year  $y$  of the reproductive population, and the term  $(\text{mean}(\beta_{x,j_1}, \beta_{x,j_2}) - \bar{\beta}_{x,y})$  is the selection differential in the breeder's equation. Parameter values used in the model are located in [Supplementary Table S1](#).

## Results

### Changes in the mean lengths-at-maturation and sex change

In all scenarios, size-selective fishing mortality drove evolutionary changes in the mean length-at-maturation and higher fishing mortality rates resulted in greater changes ([Figure 1](#)). The process determining sexual transformation had a striking impact on the direction of change in the mean length-at-maturation. Both of the critical size-at-sex change scenarios showed nearly identical increasing, almost linear trends in the mean length-at-maturity after fishing started ([Figure 1a and b](#)). Within these scenarios, changes in mean length-at-maturation were slightly greater for the static than genetically determined size-at-sex change ([Figure 1a and b](#)). Both of the social control scenarios also showed very similar trends in the mean length-at-maturation, but unlike predictions for critical size-at-sex-change scenarios, mean lengths-at-maturation were predicted to decline in response to fishing ([Figure 1c and d](#)). Within the social control models, well mixed populations were also predicted to have slightly greater



**Figure 1.** Mean length-at-maturation for critical size (left) and social control of sex change (right) for varying levels of male size advantage, ranging from weak ( $\delta = 1$ ) on the top to strong ( $\delta = 8$ ) on the bottom, from year 100 to 700 of the simulation with fishing starting in year 200. Static (column a) and genetic (column b) control of sex change and social control with well mixed populations (column c) and social control with sex-specific segregation (column d) over a range a fishing mortality rates with lighter shades indicating higher fishing mortality rates. Note that each line represents the average of 100 replicates.

changes than sex-segregated populations (Figure 1c and d). The magnitudes and rates of change in the mean lengths-at-maturation were greater for the social control scenarios.

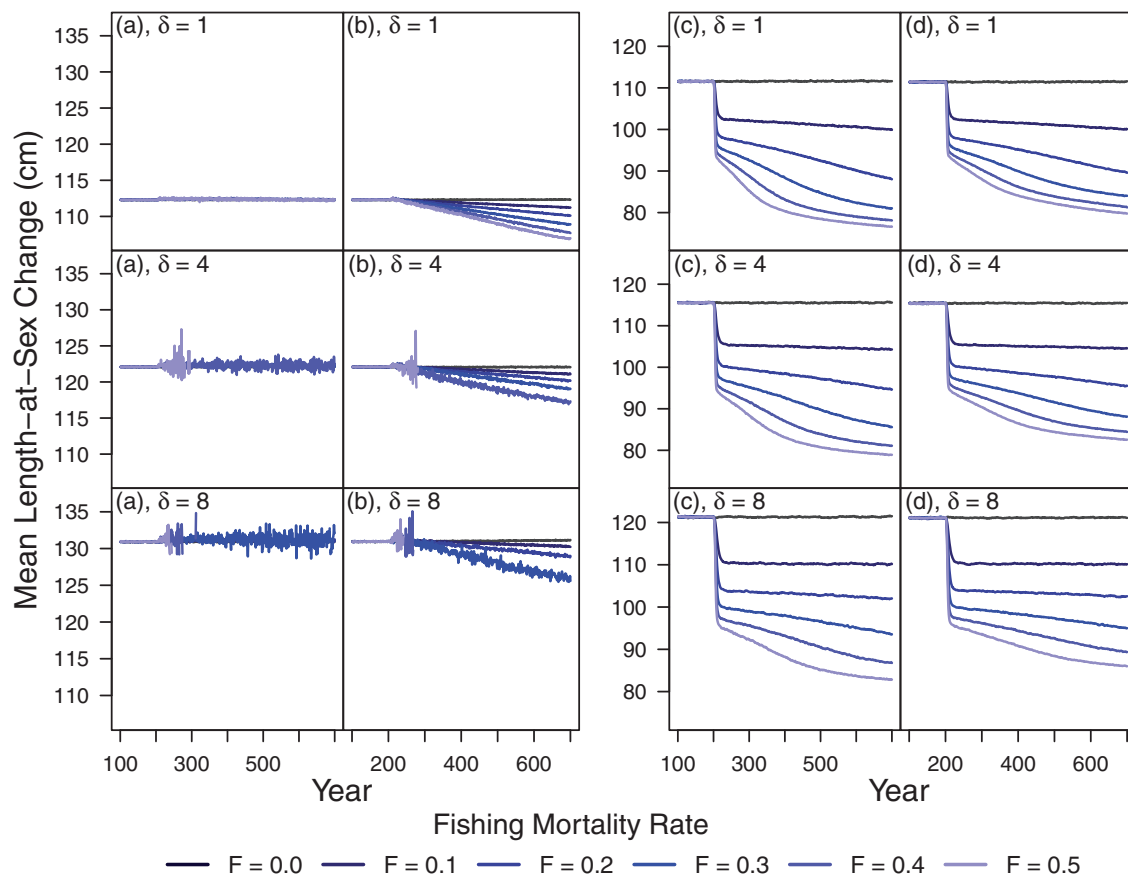
High fishing mortality rates ( $F = 0.4$  and  $0.5$ ) when males had greater size advantages ( $\delta = 4$  and  $8$ ), resulted in highly variable and unstable trends in mean length-at-maturation as a result of the low population sizes. In these scenarios, populations were often extirpated prior to year 700. Evolutionary trends in the mean length-at-maturation resulted primarily from changes in  $\beta_{1,i}$ , the intercept of the maturation norm (representing the size component of maturation) and not the slope (representing the age component of maturation), as the mean of  $\beta_{2,i}$  did not change.

For all mechanisms controlling sex change, higher fishing mortality rates resulted in greater changes in the mean length-at-sex change, except when sex change was static (Figure 2). When sex change was under genetic control, declines in mean length-at-sex change occurred slowly and very consistently, appearing linear through time (Figure 2b). For both social control scenarios, rapid declines in the mean length-at-sex were predicted during the first 10 years of fishing, decelerating during the remainder for the simulations (Figure 2c and d). Trends for both social control scenarios were similar but declines in the mean length-at-sex change were generally greater for well mixed populations (Figure 2c and d).

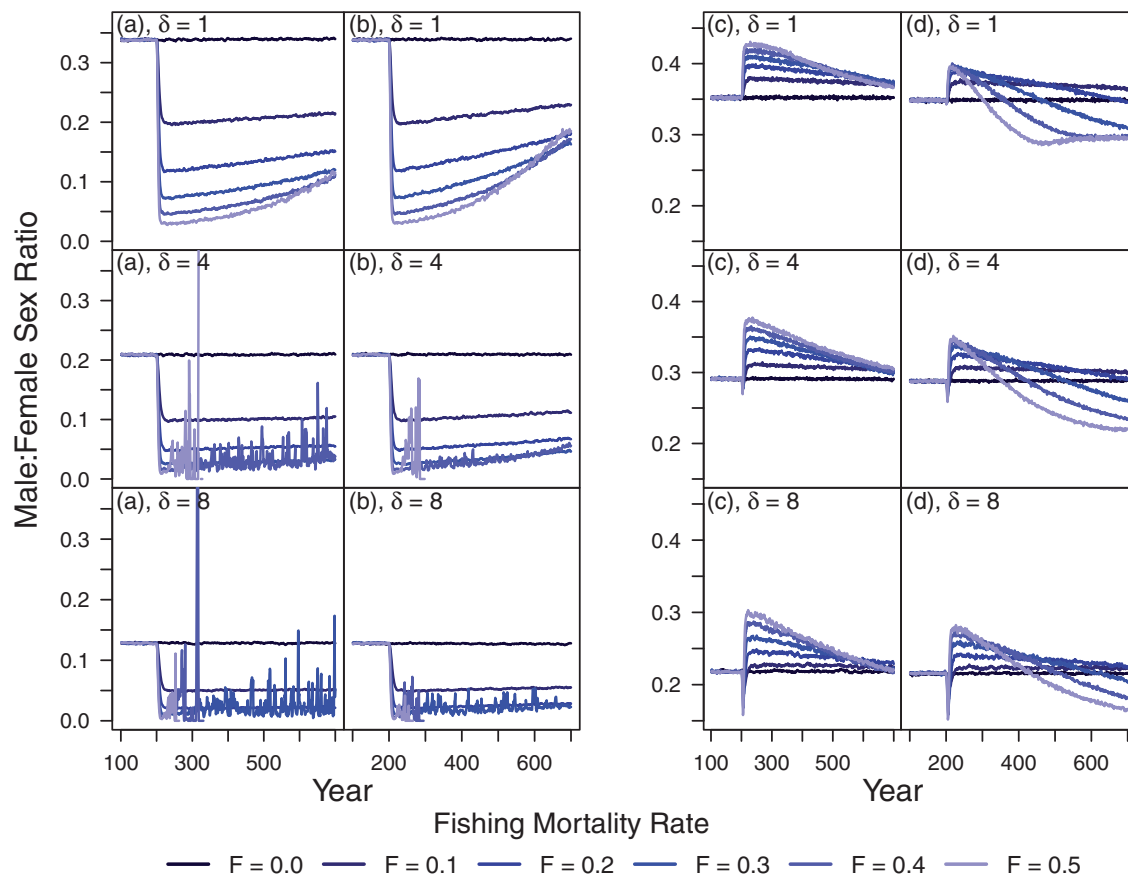
Sex change rules had different impacts on the combined effect of evolution/change in mean lengths-at-maturation and mean lengths-at-sex change. Under critical size-at-sex change scenarios the time spent in the juvenile stage increased and the mean size-at-sex change decreased (when under genetic control), effectively compressing the duration of the female stage. Under social control scenarios, the duration of the juvenile stage was reduced and the mean lengths/ages-at-maturation and sex change shifted to smaller sizes and younger ages, similar to predictions often made for dioecious species.

### Trends in population reference points

In all scenarios, the mechanisms controlling sex change had large effects on the trends in reference points after fishing. M:F sex ratios changed after the onset of fishing, but the patterns of variation through time were very different between models that assumed critical size and social control of sex change (Figure 3). As expected, decreases in the *SPR* were evident for all sex change scenarios and in all cases higher fishing mortality rates lead to lower *SPR* values (Supplementary Figure S3). Finally, reduced fertilization rates and recruitment failure only occurred when sex change was modelled assuming static or genetically controlled size-at-sex change (Supplementary Figure S4).



**Figure 2.** Mean length-at-sex change for critical size (left) and social control of sex change (right) for varying levels of male size advantage, ranging from weak ( $\delta = 1$ ) on the top to strong ( $\delta = 8$ ) on the bottom, from year 100 to 700 of the simulation with fishing starting in year 200. Static (column a) and genetic (column b) control of sex change and social control with well mixed populations (column c) and social control with sex-specific segregation (column d) over a range a fishing mortality rates with lighter shades indicating higher fishing mortality rates. Note that the scales are different between critical size and social control of sex change and each line represents the average of 100 replicates.



**Figure 3.** Male:female sex ratio for critical size (left) and social control of sex change (right) for varying levels of male size advantage, ranging from weak ( $\delta = 1$ ) on the top to strong ( $\delta = 8$ ) on the bottom, from year 100 to 700 of the simulation with fishing starting in year 200. Static (column a) and genetic (column b) control of sex change and social control with well mixed populations (column c) and social control with sex-specific segregation (column d) over a range of fishing mortality rates with lighter shades indicating higher fishing mortality rates. Male:female sex ratios for static control of sex change approach one for  $\delta$  values of 4 and 8 at fishing mortality rates of 0.40 and 0.50 (column a). Note that the scales are different between critical size and social control of sex change and each line represents the average of 100 replicates.

Similar to patterns in mean lengths-at-maturation and sex change, patterns in M:F sex ratios were clear within and between the critical size and social control scenarios. For critical size scenarios, M:F sex ratios initially declined and remained lower than the unfished M:F sex ratio, meaning fewer males per female in the populations following the onset of size-selective exploitation (Figure 3a and b). These trends were almost identical between static and genetic critical size-at-sex change scenarios, where M:F sex ratios rapidly declined after the start of fishing and shortly after M:F sex ratios stabilized/increased through time (Figure 3a and b). For populations with social control of sex change, M:F sex ratios fluctuated, but often remained closer to the unfished values than the critical size-at-sex change scenarios (Figure 3). M:F sex ratios for social control scenarios generally increased after fishing started and were followed by subsequent declines through time (Figure 3c and d). For the sex-segregated populations, the M:F sex ratios often declined to values below the unfished ratios (Figure 3c and d).

## Discussion

To fully understand the consequences of size-selective fishing mortality on sex changing fish, the evolutionary impact on life-history-traits as well as mechanisms that determine the mean length-at-sex

change must be considered. By incorporating alternative rules of sex change into our models, we have identified very different patterns of evolution in the mean lengths-at-maturation and sex change as well in various population reference points. When assuming critical size-at-sex change, even when that size had a genetic basis, the model showed relatively slow changes in the mean lengths-at-maturation and sex change. This slow response to size-selective fishing resulted in lower M:F sex ratios, the potential for sperm limitation, and high probabilities of recruitment failure, which were similar to predictions in other studies in which sex change was held static or was slow to respond (Huntsman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004, 2005; Brooks *et al.*, 2008). Conversely when assuming social control of sex change, the model predicted rapid changes in the mean length-at-sex change, substantial decreases in the mean length-at-maturation, and increased M:F sex ratios. The high plasticity in sex change prevented both sperm limitation and recruitment failure when sex change was socially controlled. Similar to Alonzo and Mangel (2005) our results support the need for a better understanding of sex change rules to predict not only the response to size-selective fishing, but also the impacts of different management strategies.

Many studies have identified decreases in the size/age-at-maturation and sex change in exploited hermaphroditic fish and

shellfish populations (e.g. Hamilton *et al.*, 2007; Collins and McBride, 2011; Fenberg and Roy, 2012; Mariani *et al.*, 2013), suggesting the potential for fishery-induced-evolution. Until recently, few simulation studies have assessed the evolutionary impacts of size-selective fishing mortality on sequential hermaphrodites (e.g. Sattar *et al.*, 2008). Assessing the evolutionary impacts of fishing has mainly been confined to dioecious (i.e. separate sex) species. These studies have shown decreases in the mean length-at-maturation associated with size-selective fishing mortality (e.g. Jørgensen, 1990; Rijnsdorp, 1993; Grift *et al.*, 2003; Olsen *et al.*, 2004, 2005), similar to the findings presented in this study with socially controlled sex change. However, the predicted maturation trends for the critical size models (i.e. static and genetic control of sex change) were very different from those produced by socially controlled sex change. For both the static and genetic control of sex change models, the mean length-at-maturation increased as a result of exploitation. When sex change was under genetic control, size-at-maturation eventually decreased but only after more than 50 generations of fishing (see Supplementary Figure S5). The differences in maturation trends between the critical size and the social control of sex change models reflect a trade-off between survival, growth, and the reproductive schedules.

Life-history-theory predicts that exploitation will usually cause earlier maturation (Gross, 1985; Law and Grey, 1989; Rowell, 1993; Roff, 2002; Ernande *et al.*, 2004). Individuals that mature early will be favoured over late maturing individuals as a result of reduced life expectancy from exploitation (Gross, 1985; Law and Grey, 1989; Rijnsdorp, 1993; Rowell, 1993; Law, 2000). These predictions have been corroborated by many empirical studies on dioecious species (e.g. Rijnsdorp, 1993; Trippel, 1995; Conover and Munch, 2002; Olsen *et al.*, 2004, 2005; Mollet *et al.*, 2007; Pardoe *et al.*, 2009) and the modelling study by Sattar *et al.* (2008) on hermaphrodites. These same predictions result from our models assuming social control of sex change and from the long-term simulations assuming genetic control of sex change (see Supplementary Figure S5). Results from the shorter term simulations of the model assuming genetic control of sex change did not conform to the predictions from life-history-theory. When sex change was genetically controlled, the ability to sex change was dependent on attaining a critical size. Therefore, decreases in the length-at-maturation increase the probability of surviving to reproduce as a female (a fitness advantage), but also increase the time (and probability of mortality) it will take to reach the size required to change sex (a fitness disadvantage if males have high reproductive success). Because growth rates were higher for juveniles, a larger length-at-maturation allows individuals to maintain higher growth rates for longer and thus, have a greater chance of becoming a male (a fitness advantage even at the expense of not surviving to reproduce). Interestingly this trade-off was not present with the social control model because individuals did not need to attain a critical size to change sex and those individuals that were able to reproduce prior to entering the fishery had higher reproductive success.

The sex change rules compared in this modelling effort resulted in widely differing magnitudes and trends in the mean size-at-sex change and M:F sex ratios. The interesting differences arise immediately after fishing started in year 200. Genetically controlled sex change models showed a consistent decrease through time, whereas socially controlled sex change showed an abrupt drop in the mean length-at-sex change after the initiation

of fishing as a result of changes in population structure. It was also evident that M:F sex ratio trends varied based on sex change rules. Short-term trends in M:F sex ratio for the critical size-at-sex change models were always decreasing, resulting in more females per male. For the social control models, we saw the opposite short-term trends. In general, M:F sex ratios increased, resulting in more males per female. These short-term trends in maturation, sex change, and M:F sex ratios present interesting implications for the ability to detect differences in the sex change rules.

For many exploited hermaphroditic species, it can be difficult to determine the sex change rules to inform management and assessment models. The trends in the mean size-at-sex change and M:F sex ratio predicted from this model could be used to hypothesize sex change rules for exploited species. If there are abrupt changes or spatial differences in fishing mortality, identifying whether sex change is based on a critical size or social control should be possible. For example, there are large spatial differences in the mean length-at-sex change in hogfish in which males inhabiting nearshore reefs on the Florida Coast are substantially smaller than those occupying offshore reefs (Collins and McBride, 2011). These differences are thought to be a result of heavy recreational spear fishing on the nearshore reefs and as a result, the mean lengths-at-sex change were almost 26 cm smaller for those reefs (i.e. 33 vs. 59 cm for nearshore and offshore reefs respectively; Collins and McBride, 2011). Along with the differences in the size-at-sex change, hogfish are harem protogynous hermaphrodites and males and females inhabit the same habitat throughout the year (Collins and McBride, 2011, 2015), suggesting social control of sex change with relatively low uncertainty of when to change sex. On the other hand for gag, a lekking protogynous hermaphrodite in which females and males do not occupy similar habitats during the non-spawning season, the mean length-at-sex change has been relatively stable since the 1970s (SEDAR, 2014). Additionally, the M:F sex ratios for gag, which were initially quite female-biased, drastically dropped from ~18% males in the 1970s to around 1% in the 1990s (Coleman *et al.*, 1996; McGovern *et al.*, 1998), suggesting genetic control of sex change. Of course, only a few sex change rules have been compared in this study and other rules should be considered in future studies.

Many sex change rules have been developed and used to describe the patterns of sex change for hermaphroditic species. The hypothesis that developmental processes (e.g. a critical size or age) initiates sex change is a common assumption for many assessment and population models (e.g. Armsworth, 2001; Alonzo and Mangel, 2004; Brooks *et al.*, 2008; SEDAR, 2014). This assumption ignores the possibility that size-at-sex change should correspond to maximizing reproductive fitness (Munday *et al.*, 2004) and is influenced by the social structure of the population (Shapiro and Boulon, 1982). The size advantage model, which was used in this study to describe social control of sex change, predicts that individuals will change sex when they can improve their reproductive fitness (Ghiselin, 1969; Warner, 1975, 1988; Warner *et al.*, 1975; Charnov, 1982b) and often occurs in response to social cues, behavioural responses, or demographic changes (Warner, 1988). In both of the social control models, we assumed that individuals had perfect knowledge of the population. This is not an accurate reflection of reality and uncertainty in when to sex change would have likely resulted in slower changes in the mean lengths-at-maturation and sex change.

Additional work will be needed to fully understand the evolutionary and population-level effects of uncertainty for populations with socially controlled sex change.

Over the range of fishing mortality rates used in this study, populations with socially controlled sex change were much less likely to experience recruitment failure (see [Supplementary Figure S4](#)). Further, these populations were able to persist at fishing mortality rates that caused extinction in populations with critical size-at-sex change scenarios. However, at low fishing mortality rates, populations with critical size-at-sex change had higher *SPR* values than those with social control (see [Supplementary Figures S3 and S4](#)), similar to [Huntsman and Schaaf \(1994\)](#) and [Alonzo and Mangel \(2005\)](#). Rapid decreases in the mean length-at-sex change for social control scenarios lead to greater reductions in egg production than critical size of sex change populations because females transition to male at smaller sizes. This trend was reversed at high exploitation rates where populations with critical size-at-sex change were much more likely to suffer from recruitment failure and/or experience sperm limitation (see [Supplementary Figure S4](#)). These results suggest that assuming static maturation and/or sex change schedules would be appropriate for modelling short-term population dynamics, such as those used in fishery stock assessment models, when sex change and maturation are genetically determined. However, this assumption would not be appropriate to make when modelling dynamics of species in which sex change is under social control.

Comparing results from this study with findings from similar models of dioecious species show some notable similarities in the evolution of maturation reaction norms. The first was evident in the evolution of the maturation reaction norm intercept and slope (representing length and age components respectively). Evolutionary models for dioecious species have consistently identified evolution in the intercept, but little to no evolution in the slope of the maturation reaction norm (e.g. [Dunlop et al., 2009](#); [Enberg et al., 2009](#); [Eikeset et al., 2016](#)), as was identified from both critical size and social control of sex change scenarios. Second, when maturation evolved along with other traits, such as growth characteristics (e.g. growth capacity, asymptotic size, growth rates, etc.), reproductive investment, and/or energy acquisition, studies have consistently found less evolution in the maturation schedules compared with those where only maturation evolved (i.e. [Wang and Höök, 2009](#); [Kuparinen and Hutchings, 2012](#); [Eikeset et al., 2016](#); [Mollet et al., 2016](#)). This is similar to what was observed in scenarios where the critical size-at-sex change evolved, further highlighting the trade-offs and interactions between reproductive schedules, growth, and survival on the evolution of maturation schedules identified in [Wang and Höök \(2009\)](#) and [Eikeset et al. \(2016\)](#), and this manuscript. Given these similarities in the evolution of the maturation reaction norm between dioecious and hermaphroditic species it would be informative to assess the evolution of additional parameters, such as female/male reproductive investment or growth characteristics in sequential hermaphrodites.

Density-dependence was incorporated through the stock–recruitment relationship via higher offspring mortality at higher levels of fertilized gametes, but for simplicity we chose not to incorporate density-dependent growth. Recent studies on dioecious species have consistently found less evolution in maturation from exploitation when density-dependent growth was incorporated into evolutionary models ([Dunlop et al., 2015](#); [Eikeset et al., 2016](#)). We would expect to see similar trends in the evolution of

maturation in sequential hermaphrodites. For critical size-at-sex change models we would also expect that density-dependent growth would help with population persistence at high exploitation rates (e.g. [Eikeset et al., 2016](#)) and decrease the likelihood of sperm limitation. The magnitude of density-dependent growth has also been found to influence evolutionary trends (i.e. there appears to be a negative correlation between the magnitude of density-dependent growth and evolution, with the greatest evolution occurring with no density-dependent growth) and population persistence in response to fishing ([Dunlop et al., 2009, 2015](#); [Lester et al., 2014](#); [Eikeset et al., 2016](#)). However, we do not know the magnitude of density-dependent growth in Gag or other hermaphroditic species. Therefore, it is clear that additional work is needed to predict how the magnitude of density-dependent growth impacts fishery-induced evolution and trends in population reference points of sequential hermaphrodites.

Many sequentially hermaphroditic marine organisms are targeted in recreational and/or commercial fisheries and the mechanism determining when individuals change sex is often unknown. As a result, there has been uncertainty around how sequentially hermaphroditic populations evolve and change in response to size-selective exploitation. When using population and assessment models for these species, it is common to make the simplifying assumption that maturation and sex change are static because the species-specific sex change rules are unknown (e.g. [Alonzo and Mangel, 2004](#); [Brooks et al., 2008](#); [SEDAR, 2014](#); [Provost and Jensen, 2015](#)). By considering multiple transition rules, we showed very different evolutionary trends in reproductive schedules and trends in population reference points as a result of size-selective fishing mortality. These differences in sex change rules not only highlight the need for a better understanding of the mechanisms controlling sex change, but also provide tools that could be used to help predict the possible sex change rules for exploited species.

## Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

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